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AN ANALYSIS
OF THE FUNCTIONAL DIFFERENCES BETWEEN THE CONTRACTIONS OF THE ADDUCTOR MUSCLES IN THE THORACIC LEGS OF THE LOBSTER
HOMARUS VULGARIS L.[1]

by

C. A. G. WIERSMA

California Institute of Technology, Pasadena;

(*From the Laboratory of Comparative Physiology, University of Utrecht*)

INTRODUCTION

In a previous article (WIERSMA, 1951) mention has been made of the remarkable difference found in the reaction of the muscles closing the various claws of *Homarus* to stimulation of the nerve fiber for the fast contraction. It was observed, that, whereas the closer muscles of the small claws of the second legs reacted with a clear "twitch" contraction to single shocks, this was not the case in the two chelipeds. But of these the cutter claw was found to give a very strong contraction on two shocks in close succession, whereas the crusher claw did not noticeably react on even two shocks. The present paper will give a more detailed description of these differences, and throw some light on factors involved in bringing them about.

METHODS

The legs of the lobsters were isolated by making them autotomize at the junction of the baso- and ischiopodite. The nerve was exposed by removing the ventral half of the shell of the meropodite, sparing the regions near the joints, and removing the muscles. In most instances the

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[1] The author wants to express his sincere thanks for the hospitality and cooperation received from Professor Dr. S. DIJKGRAAF and the staff of the Laboratory.

fast fiber for the closer muscle was prepared as a single unit. In the 2nd to 4th leg this is easier to perform without undue stimulation of the muscle than in the claws, especially the crusher. In the legs a single induction shock to a nerve bundle is sufficient to show, whether or not the fiber is present in it, but faradic stimulation is needed for the crusher claw. Furthermore it is especially difficult to decide for this claw whether the slow or the fast fiber is being stimulated. Once the bundles are thin enough so that single fibers can be spotted the distinction between slow and fast becomes somewhat clearer as the slow is thinner than the fast fiber, but until both axons are single units this indication can sometimes be misleading.

The experiments performed can be divided into two groups. In the first the mechanical contractions were registered, in the second the action potentials. Stimulation of the axons was performed in the first group in two main ways. In one set two primary induction coils, each with its own battery, shared one secondary coil placed in a symmetrical position between the primaries. This secondary coil was connected to micromanipulated stimulating electrodes. The timing of the two impulses was obtained by means of a Lucas contact breaker, by which the interval between shocks could be varied between 0 and 36 milliseconds. In the other method the effect of two, three or four shocks separated by intervals of 4 milliseconds were compared with each other. These 4 shocks were derived from 4 primary induction coils, all connected to the same stimulating electrodes by means of two secondary coils, care being taken that in all circuits the polarity was identical. As in the first instance the primaries were activated by breaking a current flowing through them with the aid of a spring driven arm, which knocked out a contact in the circuit. Registration of the contraction was most often isotonic, only in some instances was isometric registration necessary.

In the set of experiments, in which the action potentials were studied, the Lucas pendulum has been used, in some cases in the manner described above, but in addition as a device to obtain short duration rather high frequency sinusoidal stimulation. The instrument providing the latter was a Philips audiofrequency generator. The frequency was set most often at either 200 or 400 per second and by letting these stimuli pass through the preparation for the time set by the Lucas pendulum the number of resulting nerve impulses could be fairly well regulated. In some instances stimulation has been with the stimulator alone at a frequency of 20 per second.

The indifferent recording lead was invariably located at the tip of the pollex in all legs with claws. In the fourth leg a hole was made below the closer tendon in the corresponding place. The proximal lead was always on the underside of the propodite, near to its junction with the carpopodite. Similar leads were widely used in previous experiments on other species. The action potentials were recorded with the aid of a Philips cathode-ray oscillograph and photographed on paper with a horizontal camera[1].

RESULTS

The experiments with mechanical contractions have on the whole confirmed the preliminary findings (WIERSMA, 1952). In most preparations single impulses in the fast closer fiber of the second leg cause an easily observable contraction, which often is rather difficult to record, especially after some fatigue. If two impulses are given 1.5 or more milliseconds apart a stronger contraction is observed in the freely contracting claw, and this contraction registers much larger with the isotonic lever than the one caused by a single impulse. Summation is very pronounced up to intervals of 5 milliseconds and gradually declines with longer time intervals, being at 20 milliseconds only about half of the maximum. The third leg, which is also chelated, behaves in a similar fashion. In the fourth leg the only difference is that both types of contractions are smaller, so much so that often the reaction to a single impulse is too small to be registered, though usually visible. The contraction on two shocks is also small, and the fresh preparations very much resemble then the fatigued ones of the second and third legs. Some attempts were made to use the fifth legs, but these were rather unsuccessful, because the contractions were very small, even on two or more shocks. It may be remarked here, that in this case the preparation of separate fast and slow axons was difficult and succeeded in only a few cases. These preparations were used to investigate another problem, namely whether either of the two movements gave rise to a rotation of the dactylopodite. The fifth leg of *Homarus* has the remarkable feature that the joint between pro- and dactylopodite is loosely constructed, so that the dactyl can lag behind over an arc of about 30° as the animal walks. In similarly formed joints between the carpo- and propodite in the walking legs of *Dardanus* and of *Dromidiopsis* it was shown (WIERSMA and RIPLEY, 1954) that rotation in one direction took place on stimulation of the fast, in the other direction on slow contraction. No such difference in movement could be observed in this leg, both contractions seemingly moved the dactyl absolutely straight with regard to the propodite. It is likely that only the dragging effect of the bottom surface causes rotation here.

The effect of two shocks, no matter how short the time interval, never has led to any noticeable contraction of the crusher claw, but in the majority of the cutter claws, a large contraction appears under these circumstances when the shocks are closely spaced. In some cutter claws there is a just noticeable contraction on single impulses, which can be registered under isotonic conditions without load. A very similar contraction is then visible when the interval between the two shocks is 20 milliseconds, but with shorter intervals the contraction rapidly increases and at about 12 milliseconds the claw closes completely. In order to show that shorter intervals result in still stronger contractions, it is necessary to use isometric registration or to apply a load. Under both conditions the contractions obtained with intervals between 1.5 and 4 millisecond are maximal, with a gradual decline in strength with longer intervals. However, fatigue will gradually diminish the contraction heights and often will also lengthen the refractory period of the preparation, so that the latter may become as long as 3 milliseconds instead of the original 1.5 (c.f. WRIGHT and COLEMAN, 1954).

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[1] I am much obliged for the help of Mr. J. STOPPELS with the taking of these pictures.

By using 3 and 4 impulses instead of 2 it can be determined in how far the twitches obtained on 2 impulses are near the maximum which the muscle can give. In case of the 2nd, 3rd and 4th thoracic legs, the result usually obtained is, that there is an increase in strength of about the same order for each additional impulse. Table I shows that the contraction, at least when registerd with a lever, is considerably larger on two impulses than on one, but that 3 and 4 give further stepwise increases of approximately equal magnitude. In the crusher claw 3 impulses may cause a noticeable contraction under isotonic conditions without load, which approximately doubles in height with 4 impulses. But in some cases such contractions could not be obtained and it was then necessary to give a preceding faradic stimulation to the fiber in order to show that during the post tetanic facilitation, contractions on 3 or 4 impulses were present. On the other hand, when the contraction of the cutter claw on two impulses is well developed, isometric regis-

TABLE I

Comparison between the contraction heights obtained by 1 to 4 impulses in the different legs. The heights are isotonic deflections in mm except for the cutter claw which are isometric in grams. All values are uncorrected, 4 msec between shocks.

No. of impulses	1	2	3	4
Leg 4	0 mm	3	5	12
Leg 3	1	15	25	35
Leg 2	1	17	34	55
Crusher claw	0	0	7	12
Cutter claw	0 g.	100	125	140

tration shows, that 3 and 4 impulses only increase the tension developed by a relatively small percentage. But when two impulses through previous fatigue give only a small contraction, three impulses will develop a very pronounced increase, whereas the result of 4 may remain little changed compared to the unfatigued state. An exception to this rule was found in one cutter claw, which was in shape somewhat closer to a crusher than is normally the case, having a pronounced tooth on the inside of the pollex, but being still much more slender than the crusher claw, which appeared to be normal. In this case, there was a much more gradual increase in strength, 2 impulses giving a very small contraction, 3 an intermediate and 4 a rather strong one, but not yet strong enough to close the claw.

In the experiments, in which action potentials were led off, a close parallelism was observed between the potentials obtained and the type of contraction elicited.

In case of the 2nd and 3rd legs single impulses resulted in a small diphasic action potential, double impulses in action potentials which invariably showed two diphasic potentials, the second one considerably larger than the first, its height diminishing, however, when the spacing became longer (fig. 1). When more impulses followed each other, as by use of the audio generator, the facilitation of the diphasic potentials went on for a considerable time, and would remain after stimulation had stopped as could be shown by giving a single impulse after a short interval. Under such circumstances both the diphasic action potential and the twitch contraction can be many times that of the preparation in the non-facilitated state.

The action potentials of the cutter claw differ noticeably from this picture. As is shown in fig. 2, single impulses result in an almost completely monophasic potential, but when two impulses follow each other quickly a large diphasic deflection occurs on the second shock. With longer intervals this deflection becomes dispersed and there is a tendency to polyphasicity, whereas the twitch becomes smaller. With still longer intervals, when no visible contraction takes place, the quick diphasic potential is again absent. The action potentials of the fourth leg are somewhat similar to those of the cutter, in that a clear diphasic potential occurs here too, only on the second impulse but the relative size of this deflection is much smaller. When subsequent impulses are given, the potentials of the fourth leg show, however, a very considerable facilitation, whereas in the cutter claw there is only relatively little subsequent growth.

The crusher claw gives action potentials even on two shocks which do not ever show any noticeable quick diphasic deflections. Instead a summation and facilitation of a monophasic deflection is here the main result. This picture is almost identical with that obtained in a slightly fatigued fourth leg. It also resembles strongly the action potentials obtained previously in *Blepharipoda* (fig. 3) and *Randallia* (WIERSMA and VAN HARREVELD. 1938a). However in contrast to the latter the monophasic deflections of the crusher are never accompanied by a twitch and furthermore the crusher claw shows diphasic potentials when more impulses are given.

DISCUSSION

Though there are still several important clues lacking, it seems useful to discuss at present our knowledge of the relation between crustacean muscle action potentials and contraction. The reasons why this relation is so difficult to explore are several. Crustacean muscle fibers can, by histological methods, be shown to receive, on the one hand two or more motor axons, and on the other each of these axons makes many connections along the length of each fiber. To a certain degree, the physiological findings are now in accord with this concept. By the use of internal electrodes it has been shown (FATT and KATZ, 1953) that when stimulation of a motor fiber causes so called "local" or "end plate potentials", these are observable throughout the muscle fiber and not in one end plate region, as in mammalian striated muscle fibers. It has also been possible to observe this type of potential in a single muscle fiber, upon stimulation of either of two motor axons (FATT and KATZ, 1953, FURSHPAN and WIERSMA, 1954). The two potentials differ from one another, in that one can be obtained on single nerve impulses, whereas the other does not show unless several impulses follow each other rather quickly. The first, the large local potential, occurs when the fast nerve fiber is stimulated, the second, the small local potential, when the slow is excited. These results are in complete accord with the picture obtained with external electrodes, applied in the way as used in this investigation.

But especially in the fast system, internal electrodes show clearly, that in addition to the "local" potentials, spikes can occur, which differ from the local potentials in being often larger than the membrane potential. These, in certain fast systems, are present even on single impulses, whereas in other cases they do no appear unless two or more impulses have first caused summation of the local responses. However, it was found, that the appearance of spikes is not a simultaneous process in all muscle fibers of a muscle, but that depending on the circumstances e.g. of the spacing of two impulses, fewer or more fibers of the muscle can give this phenomenon. To further confuse this issue, spikes do not seem to be always all-or-none processes, as abortive spikes were sometimes obtained in fibers, on two impulses following each other at an interval somewhat longer than one which gives a full fledged spike. Under these circumstances then, the muscle as a whole will show heterogeneity with regard to the potentials of its muscle fibers. Unless the contraction of each fiber can be registered at the same time as the potential, it will not be possible to definitely state which of the potentials is accompanied by a twitch contraction of the fiber and which one is not.

From these considerations it seemed useful to try to relate the potentials with external leads on the one hand to internal potentials, on the other to the observed muscular contractions, as they must in some way, represent the overall picture of the electrical events in all muscle fibers. When local potentials obtained by either method of leading off are compared, the results observed are usually very similar. Thus the potentials obtained on stimulation of the slow fiber correspond in amounts of facilitation and relative sizes. The same is true for local fast potentials. But in the case of spikes, this correspondence seemed to break down, as WIERSMA and VAN HARREVELD (1938a) found that in *Randallia* and *Blepharipoda* the fast potentials showed monophasic potentials, which summated always smoothly, without any sign of a sudden change in process (fig. 3), whereas with internal leads in other muscles of other species spikes are easily obtained on similar stimulation. The absence of spikes with external leads in the two species was the more remarkable, because the smaller potentials on single impulses were without an accompanying twitch, whereas those on two or more closely spaced impulses were of the same shape but followed by a strong twitch. Hence, the conclusion was drawn at that time, that all twitches were accompanied by local fast potentials. This view was to a considerable extent strengthened by the observations made on the closer muscle of the crayfishes, in which there was seemingly very little difference between the external action potentials accompanied by twitches, and those in which the twitch had disappeared by "fatigue", the latter being only about 10 % smaller than the former. However, with internal electrodes it was shown, that the closer of the crayfish, *Cambarus*, is exceptional in the relation between the size of the local potential and the spike, which are here very difficult to recognize, since potentials, presumably completely local may be as high as 90 % of the membrane potential. A close scrutiny of the potentials with external leads may in this case indeed give an indication of the presence of spikes in the muscle, as has been pointed out by KATZ and KUFFLER (1946) with regard to a picture obtained on two impulses in this muscle by VAN HARREVELD and WIERSMA (1936). Thus in this case there is again a correspondence between outside and internal leads. It should be remarked that for both types of lead it is (in this species) very difficult to decide when spikes are present.

If the view that external leads are able to give clear indications of the electrical events in the muscle fibers is correct, one should have no difficulty to detect spikes with external leads in cases where there is a pronounced difference between fast local and spike potentials with internal ones. And from the results observed in *Homarus*, this seems indeed to be the case. One may object that no internal leads have been used in *Homarus*, but from the results on a number of crabs there cannot be much doubt, that the diphasic deflections observed in *Homarus* were due to spikes. In *Homarus* then, there seems to be a high correlation between the occurrence of spikes, diphasic deflections in external leads and twitch contractions of the fibers giving the spikes. In the second and third thoracic legs a diphasic deflection is obtained on stimulation with a single shock, but this is rather small as is the twitch contraction and both disappear on fatigue. A second, larger diphasic deflection results from a second nerve impulse, and the height of the deflection is in agreement with the increase in height of the summated twitch contraction. In the crusher claw, on the other hand, single and also double impulses, give almost pure monophasic deflections, which summate and are not accompanied by a visible contraction. Diphasic potentials do occur at a time when contractions become visible. The case of the cutter claw is perhaps the most convincing, as here a single impulse results in almost no case in a twitch, and the action potential is almost purely monophasic, but a very strong twitch and large diphasic deflection appear on two impulses.

It seems almost inevitable to draw the conclusion that in *Homarus* and most likely also in many other decapods twitches occur only when spikes are set up. However, from the events of slow contractions it is quite evident, as also pointed out by Fatt and Katz (1953), that local potentials must be able to cause muscular contractions, even though under circumstances of high frequency stimulation, spikes may also occur on stimulation of the slow fiber. Considered in this way, the paradox of the fast and slow contractions (Wiersma and Van Harreveld, 1938b) may be stated: why do large fast locals not cause contractions whereas slow small locals do? By accepting different transmitters for the two systems (Florey and Florey, 1954) a certain likelihood for such an occurrence may be present, though not obvious. At present, there is no reason to believe, that at least in *Randallia* and *Blepharipoda* fast local potentials do not give rise to twitches, on the contrary all indications are that they do. Experiments to further investigate this with internal electrodes are planned. It seems likely that there are in this respect great species differences, and that it is these differences which have confused the issue.

With regard to our original query, about the relation between con-

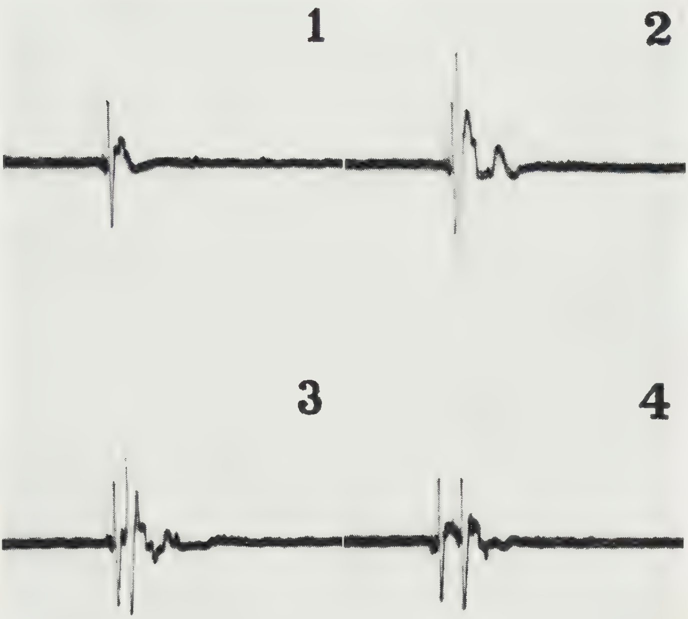

Fig. 1. Action potentials from closer muscle of the third leg, with double shock stimulation. The interval between shocks was as follows 1 : 2 millisec.; 2 : 4 millisec.; 3 : 10 millisec.; 4 : 20 millisec. In 1 a small twitch accompanied the single action potential, the second shock falling in the refractory period of the nerve. In 2 a large twitch occurred, which was somewhat smaller in 3 and in 4 only slightly larger than the simple twitch in 1. Time is indicated by the distance of the two tops in 4.

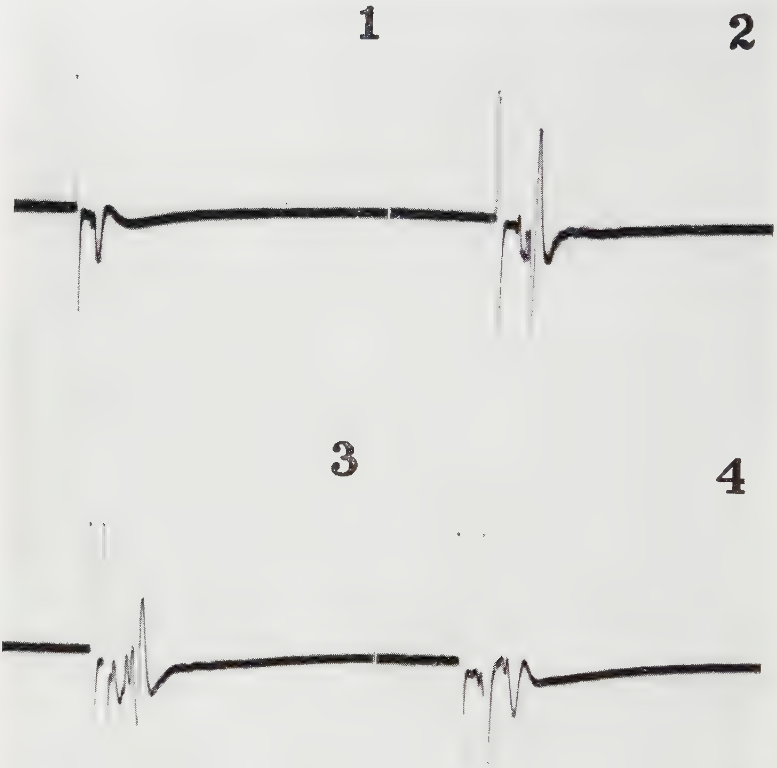

Fig. 2. Action potentials from the cutter claw, on double shock stimulation. Interval between shocks: 1: single shock; 2: 2 millisec.; 3: 10 millisec.; 4: 20 millisec. Compared to fig. 1 polarity of leads was reversed. In 1 no visible contraction occurred, in 2 a strong twitch appeared, in 3 a weak contraction and in 4 no contraction was observable. Notice the monophasic deflection in 1, whereas in 4 the second impulse causes a slightly more diphasic deflection. Notice that in this record the stimulation artifacts are much larger than in fig. 1. Time as in fig. 1.

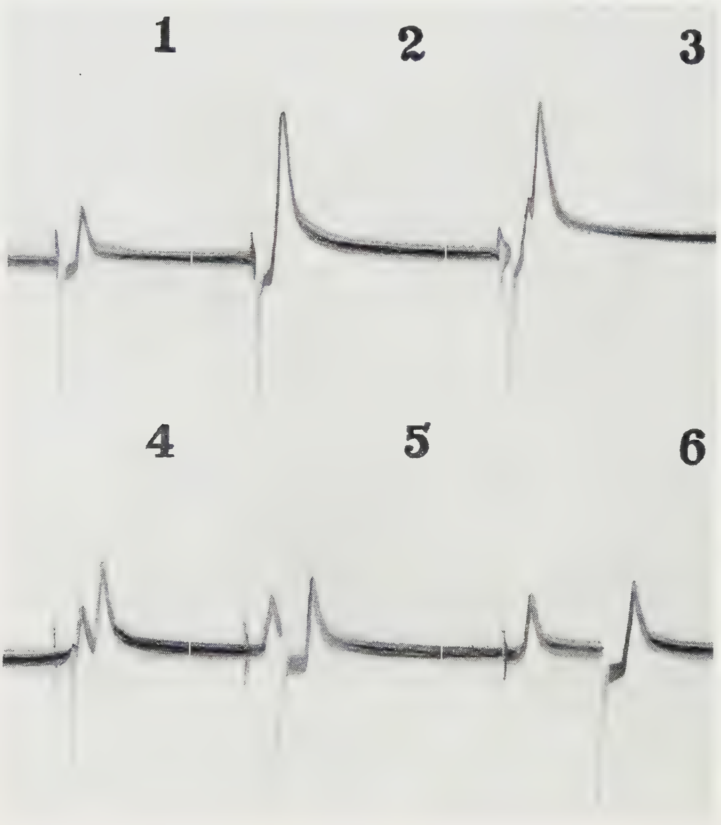

Fig. 3. Action potentials from the closer of the claw of *Blepharipoda occidentalis* on double shock stimulation (Rearranged from Wiersma and Van Harreveld, 1938 a, p. 22). 1: Interval between shocks 1.4 millisec.; 2: 1.6 millisec.; 3: 3.6 millisec.; 4: 7.2 millisec.; 5: 14.4 millisec.; 6: 34 millisec. From the records it appeared that 1, 5 and 6 were not accompanied by a visible contraction, whereas 2 showed a strong twitch, which was about of the same size in 3 and considerably smaller in 4. Time given by shock intervals.

traction and muscle action potentials, the only claim that can be made on the basis of the present investigation, is that external leads do give a better picture of the overall events in the muscle than has been accepted, as they do seem to indicate the presence or absence of spikes. The fundamental difficulty of the relation between action potential and contraction remains, and will remain until the above mentioned paradox and the results of inhibition can be explained.

In the mean time, the differences between the different muscles of *Homarus* raises other problems, which may be less fundamental but nevertheless of considerable interest. How can it be that part of the muscle fibers of the second and third leg respond with spikes to single impulses, when practically none in the cutter claw do so, whereas a second impulse recruits relatively few fibers in the legs and practically all in the claw? Furthermore, in young lobsters, the two claws are similar in shape and resemble the cutter claw, later they become differentiated, sometimes the left, other times the right becoming a crusher claw. As Emmel (1908) has shown one can influence this development by removing one of the claws during the first four moults, in which case the remaining claw will differentiate to a crusher. But after the fifth moult the pattern seems very stable, once a leg has differentiated, it usually regenerates as the same type in older animals. It is interesting to note that from an anatomical standpoint only the crusher is specialized, but that in physiological respects both claws have special properties, and that in one case, in which an intermediate between the two types seemed to be present from an anatomical point of view, this claw behaved physiologically much as the posterior thoracic legs.

SUMMARY

The different thoracic legs of the lobster *Homarus vulgaris* have been compared with regard to the contractions caused in the closer muscles on one and more impulses in the "fast" nerve fiber.

It was found that small twitches occurred in the fresh preparations especially in the second and third legs; that the cutter claw, the fourth and fifth leg showed sometimes a very small contraction on a single shock, but that in the crusher claw more than two closely spaced impulses are necessary before a visible contraction occurs. Two closely spaced impulses in the second, third and fourth leg lead to a stronger twitch, which increases considerably in strength on further impulses. In the cutter claw two such impulses lead to a very strong twitch, which increases but little with a greater number of impulses.

Muscle action potentials lead from the muscle with external leads

show a good correspondence between the occurrence and size of diphasic deflections and height of the twitch contractions.

These results are considered in the light of internal and external leads obtained from similar muscles of other animals and the difficulties to obtain a consistent picture between the relation of muscle action potentials and contraction in the decapod crustaceans is pointed out.

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L'INFLUENCE DE QUELQUES SUBSTANCES PHARMACOLOGIQUES SUR LES MOUVEMENTS DES CILS VIBRATILES DES TENTACULES DE METRIDIUM SENILE (L.)

par

J. TEN CATE, H. E. COOMANS ET J. N. WALOP

(*Laboratoire de Physiologie Comparée, Université d'Amsterdam*)

Les substances cholinergiques et adrénergiques qui jouent un rôle important dans la régulation nerveuse de la fonction de divers organes ont été peu étudiées jusqu'à présent quant à leur action sur les mouvement des cils vibratiles. Ainsi qu'on le sait, chez la plupart des animaux le système nerveux est sans influence sur les mouvements des cils de l'épithélium. C'est pour cela que les études de Kordik, Bülbrink et Burn (1952) qui ont cherché à mieux connaître l'action de l'acétylcholine, de l'adrénaline et quelques autres substances sur les mouvements des cils de l'oesophage chez *Rana* et ceux de la trachée chez le Lapin, ont une si grande importance. Ensuite, l'action de l'acétylcholine sur les mouvements des cils des lamelles branchiales de *Mytilus* a été examinée en 1953 par Bülbrink, Burn et Shelley.

Ces expérimentateurs ont déterminé que l'acetylcholine, de même qu'une choline-acétylase et une choline-estérase sont présents dans le tissu des cils vibratiles. Ils supposent que l'acétylcholine agit comme une hormone locale qui est synthétisée sur place; il n'y aurait des éléments nerveux ni dans les lamelles branchiales de *Mytilus* ni dans le tissu des cils vibratiles de la trachée du Lapin.

Les auteurs précités n'ont examiné qu'un seul Invertébré, *Mytilus*, il nous a donc semblé d'importance de savoir comment réagit à l'acétylcholine et à l'adrénaline l'épithélium ciliaire d'autres Invertébrés. Nous avons étudié dans ce but l'action de l'acétylcholine, de l'adrénaline et de quelques autre substances sur les mouvements ciliaires de l'Anémone de mer, *Metridium senile*. On trouve des cils vibratiles dans beaucoup de groupes d'animaux. Une observation superficielle démontre que les cils aient deux sortes de fonctions: ils sont employés dans le déplacement de l'animal (unicellulaires, beaucoup de larves des Invertébrés). En d'autres cas l'animal peut rester lui-même immobile, mais le medium est déplacé en relation de l'animal (cils vibratiles de l'épithélium de Métazoa).

Nous avons fait nos expériences sur *Metridium senile*. Les cils de *Metridium* appartiennent au second type, mais si un tentacule de l'animal est coupé et posé sur le fond d'un vaisseau avec de l'eau de mer, il peut se déplacer par le mouvement des cils. On fait usage de ce phénomène pour mesurer la fréquence du mouvement ciliaire. La vitesse de déplacement du tentacule peut servir de mesure quant à la vitesse de vibrations ciliaires.

Les anémones de mer provenaient de la Station Zoologique du Den Helder et étaient conservées dans l'aquarium d'"Artis", Jardin Zoologique d'Amsterdam.

Nous avons pris comme object d'expérience le petit tentacule sectionné. Le tentacule isolé est mis dans un petit réservoir avec de l'eau de mer. L'organe se contracte d'abord un instant, mais se déploie de nouveau après quelques minutes. Plus tard il commence à ramper avec l'extrémité sectionnée vers l'avant. Ce mouvement n'a commencé chez quelques animaux qu'après une heure environ, mais la vitesse est toujours restée à peu près la même. La longueur des tentacules isolés ne doit pas dépasser 2 mm, mais ne doit avoir moins d'un millimètre. Si elle dépasse 2 mm, les tentacules se recourbent par contraction des muscles longitudinaux. Il en résulte que le tentacule ne rampe plus en ligne droite, mais en lignes circulaires. Cela rend beaucoup plus difficile de mesurer la vitesse du mouvement.

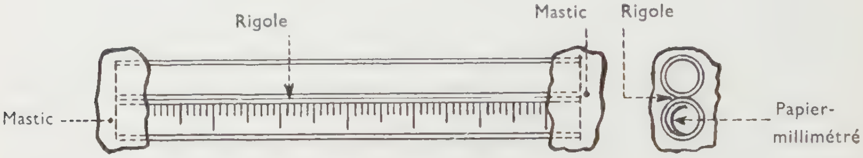
Quand la longueur des tentacules est au-dessous d'un millimètre, l'organe est plus large que long parce que son épaisseur comporte un millimètre environ. Ils peuvent alors facilement se retourner tandis qu'ils rampent et ils prennent alors une direction opposée. Ceci complique de même l'observation, parce que la vitesse doit être mesurée, c'est-à-dire le temps requis pour le parcours d'une distance déterminée.

Les tentacules ont chez *Metridium* la fonction de porter de la base du tentacule vers le haut de petites particules. La vibration active des cils est donc dirigée vers le sommet: ce dont résulte que des tentacules isolés rampent avec leurs sommet dirigé vers l'arrière. Nous n'avons jamais observé un retournement de la vibration ciliaire sur des tentacules isolés.

Vingt-quatre heures après l'isolement, les tentacules rampent encore, leur vitesse toutefois est alors quelque peu diminuée. Nous avons encore constaté des mouvements 48 heures après l'isolement, mais leur vitesse est alors très petite.

MÉTHODE

Il est important, si l'on veut mesurer la vitesse des tentacules rampants de Metridium, de les faire avancer sur une voie droite détérminée. Nous avons fait en plaçant l'un contre l'autre deux minces tubes de verre de la même dimension. Les deux extrémités étaient fixées l'une à l'autre avec du mastic.



Les tubes ont 7 cm de longueur et un diamètre de 6 mm. A l'intérieur de l'un d'eux une petite bande de papier millimétré fut placée pour pouvoir lire la distance parcourue. L'appareil était placé dans un petit réservoir contenant de l'eau de mer. L'objet étant fort petit devait en être agrandie, ce que nous avons fait à l'aide d'une loupe fixée horizontalement à un support placé au-dessus du réservoire.

Un tentacule est placé dans la rigole entre les deux tubes. Il rampe vers l'extrémité. Quand il y est arrivé à la fin il est accueilli avec une aiguille à préparation dont un seul mouvement le retourne à 180°, aprés quoi il se dirige vers l'autre extrémité.

On contrôle à l'aide d'un chronomètre à arrêt le temps qu'a nécessité le parcours de 10 mm. Entre deux observations le tentacule parcourt à peu près 5 mm que l'on ne contrôle pas; le temps qui s'écoule ainsi sert à examiner le chronomètre, noter l'observation et remettre le chronomètre à zéro.

Si le tentacule s'arrête subitement pendant une observation, ce qui arrive parfois, cette observation ne compte naturellement pas. Nous n'avons pris pour les expériences que des tentacules dont la vitesse ne s'écartait pas trop de la moyenne.

Les réservoirs qui servent à l'expérience contiennent 75 cc d'eau de mer. La substance dont l'influence sur le mouvement des cils vibratoires doit être examinée, est mise en solution avec de l'eau distillée avant le début de l'expérience.

Après avoir effectué une moyenne de 20 observations en eau de mer pure, nous avons ajouté à cette dernière l'une des solutions préparées. Après 20 observations faites dans ces conditions, le tentacule a été de nouveau examiné en eau de mer pure.

INFLUENCE DE DIFFÉRENTS FACTEURS SUR LE DÉPLACEMENT DU TENTACULE ISOLÉ

Il a été constaté que divers facteurs influencent la vitesse du déplacement des tentacules isolés de *Metridium*. La rigole doit toujours être en position horizontale. De petites souillures, pièces du mucus, bulles d'air doivent être soigneusement retirées du liquide.

Dans le but de contrôler si le retournement des tentacules a de l'influence sur la vitesse de déplacement, nous avons fait une série d'expériences pour comparer cette vitesse un instant avant le retournement avec celle observée immédiatement après.

La vitesse moyenne d'un tentacule isolé d'un mm de longueur dans l'eau de mer à 19° C comporte, avant le retournement, 18.0 sec/cm; après le retournement, elle est de: 17.0 sec/cm.

La vitesse moyenne de déplacement d'un tentacule de 1 ½ mm dans l'eau de mer à 19° C a été, avant le retournement, 23.1 sec/cm et après le retournement 24.2 sec/cm.

Ceci permet de conclure que la vitesse moyenne montre peu de différence avant et après le retournement; de plus l'on constate une fois une petite accélération et une autre fois un ralentissement du mouvement rampant après le retournement. On peut donc dire que le retournement a peu d'influence sur la vitesse de déplacement des tentacules.

Bien que la température de l'eau de mer avait été tenue constante pendant les expériences, nous avons pourtant examiné l'influence de la température sur le mouvement des tentacules, et des cils par conséquent. Ces expériences nous ont appris que la température exerce en effet une influence sur la vitesse de motilité des cils.

Dans la plupart de nos expériences la température était 20° C environ. A cette température, nous n'avons pratiquement constaté aucun changement dans la vitesse de motilité des tentacules pendant toute l'expérience. Dans la plupart des cas, la vitesse du déplacement d'un tentacule isolé de 1 ½ mm de longueur a comporté dans l'eau de mer 18–21° C, une moyenne de 20.5 à 35.5 sec/cm.

Lorsque la température monte jusqu'à 30° C, la vitesse diminue, parfois jusqu'à 85.8 sec/cm et plus; quand la température se baisse jusqu'à 5.0° C, elle atteignait en moyenne jusqu'à 45.0 sec/cm.

Ces expériences ont démontré que par élévation tout comme par abaissement de la température de l'eau de mer au dessous de la moyenne, il se présente un ralentissement des mouvements des cils vibratiles.

Si l'on ajoute à l'eau de mer une solution de la substance à examiner, il est possible que le pH de l'eau de mer change; ceci pourrait avoir de l'influence sur la fonction des cils vibratiles. C'est pour cela que nous avons mesuré le pH de l'eau de mer avant et après l'apport de la solution. Ces mesurations nous ont appris que les changements du pH survenus après l'apport des substances pharmacologiques ont peu d'influence et sont négligeables. (Le pH de l'eau de mer comportait 7.38–7.57.)

LES RÉSULTATS DE L'EXPÉRIENCES AVEC DIFFÉRENTS SUBSTANCES PHARMACOLOGIQUES

Avant de nous servir des solutions des drogues, nous avons toujours contrôlé la vitesse moyenne du déplacement de chaque tentacule. Nous avons vu que quelques heures après l'isolement, elle restait la même qu'au début. La vitesse maximale d'un tentacule a été 9.9 sec/cm.

Ainsi que nous l'avons dit plus haut, la vitesse de déplacement des tentacules isolés de *Metridium* a été mesurée 20 fois de suite dans le petit appareil, et mise en graphique. Si le résultat de l'action de la substance à examiner sur la vitesse du déplacement du tentacule ne se montrait pas assez nettement, nous avons employé la méthode de test mathématique selon *Wilcoxon* pour pouvoir nous convaincre de la signification des résultats obtenus.

Nous donnons ici en example des vitesse avec lesquelles un tentacule isolé peut se déplacer dans l'appareil, l'expérience faite avec un tentacule isolé d'un mm de longueur dans l'eau de mer pure à 17°C; 26.2; 22.4; 30.2; 33.4; 35.3; 30.3; 28.8; 25.1; 23.3; 28.1; 31.9; 32.8; 30.4; 31.2; 35.4; 36.9; 32.3; 34.7; 35.5; 32.6. La vitesse de déplacement a donc comporté en moyenne 30.8 sec/cm.

Il faut remarquer que les tentacules rampent un peu plus vite au fond du réservoir que dans la rigole de l'appareil. Ceci est causé sans aucun doute par la position moins favorablée occupée dans la rigole et non par vibration plus rapide ou plus lente des cils vibratiles.

INFLUENCE DES SUBSTANCES ADRÉNERGIQUES ET CHOLINERGIQUES

L'influence de l'adrénaline et de la noradrénaline sur le déplacement d'un tentacule isolé a été examinée dans une série d'expériences, lesquelles ont démontré que l'adrénaline et la noradrénaline en solutions de 10^{-6} et 10^{-5} exercent déjà une influence marquée sur la vitesse du mouvement ciliaire. Le tableau I reproduit quelques-unes de ces expériences.

TABLEAU I.

Expérience	t°	Longueur du tentacule	Concentration	Eau de mer	Solution	Eau de mer
11/1 '54	21°C	1 ½ mm	Adr. 10^{-6}	18.0	15.0	17.3
12/1 '54	21°C	1 ½ mm	Adr. 10^{-5}	16.6	13.5	16.0
23/1 '54	19°C	1 ½ mm	Noradr. 10^{-5}	20.9	17.0	20.0

(tous les nombres reproduisent le temps nécessaire au parcours d'un cm)

Les expériences mentionnées permettent de se convaincre facilement de ce que l'adrénaline et la noradrénaline accélèrent les mouvements des cils vibratiles des tentacules isolés de *Metridium* et qu'elles le font dès basses concentrations.

Le chlorure d'acétylcholine s'est montré d'action toute différente sur les mouvements des cils de tentacule isolé. Tandis qu'adrénaline et noradrénaline ont pour résultat une accéleration du mouvement des cils vibratiles, l'acétylcholine a toujours exercé une inhibition. De même que dans les expériences avec adrénaline et noradrénaline, nous avons toujours recherché lors d'emploi d'acétylcholine quelles étaient les plus petites concentrations de cette substance capables de provoquer l'apparition de changements dans l'activité des cils vibratiles du tentacule isolé. Ces expériences ont démontré que l'acétylcholine en concentration de 10^{-4} cause un retardement bien marqué de la vibration des cils. Une concentration de 10^{-5} a causé de même un ralentissement du mouvement ciliaire, mais pas dans tous les cas.

Les deux expériences ci-dessous peuvent servir d'exemple quant à l'action de l'acétylcholine sur les mouvements des tentacules.

TABLEAU II.

Expérience	t°	Longueur du tentacule	Concentration	Eau de mer	Solution	Eau de mer
12/2 '54	18°C	1 mm	10^{-5}	20.5	27.2	21.7
15/2 '54	18°C	2 mm	10^{-4}	16.5	32.6	23.2

(tous les nombres donnent le temps nécessaire au parcours d'un cm)

Ces expériences montrent que l'acétylcholine exerce une action nettement inhibitoire sur les mouvements des cils d'un tentacule isolé. On constate par conséquent qu'en ce qui regarde le mouvement ciliaire du tentacule isolé, l'action de l'acétylcholine est antagoniste de celle de l'adrénaline et de noradrénaline.

A côté de l'action du chlorure d'acétylcholine nous avons étudié aussi l'influence du chlorure de mécholyl sur les mouvements des cils vibratiles du tentacule isolé. Cette substance, elle aussi, a manifesté une action inhibitoire sur les mouvements des cils. Une solution de 10^{-5} en eau de mer a exercé une influence freinante marquée sur les mouvements des cils. Voici le rapport d'une expérience qui illustre cet effet du mécholyl.

Expérience du 11/3 1954; t° -19°C. Longueur du tentacule 1 mm. Concentration du mécholyl en eau de mer: 10^{-5}. Vitesse de déplacement en eau de mer pure: 23.3 sec/cm; en solution de mécholyl: 34.6/cm; en eau de mer pure: 25.8/cm.

L'INFLUENCE DE NICOTINE ET STRYCHNINE

Après avoir déterminé que l'adrénaline et l'acétylcholine ont une action nette sur les mouvements des cils du tentacule isolé, il nous a paru important de savoir si les substances pharmacologiques qui agistent sur les éléments nerveux par excellence, ont aussi une influence sur les mouvements des cils du tentacule isolé de *Metridium*. Les recherches de Leghissa (1948) ont démontré qu'il y a tissu nerveux dans les tentacules des Actinies. C'est pour cela que nous avons encore examiné quelques substances ayant une action directs sur le système nerveux des Vertébrés tout comme des Invertébrés, notamment la nicotine et la strychnine.

Ces substances alles aussi ont été appliquées en une solution de basse concentration que nous avons élevée graduellement.

Les expériences à la nicotine en eau de mer ont démontré qu'en concentrations de 10^{-6}, 10^{-5}, et 10^{-4} cette drogue n'a pas d'influence sur les mouvements des cils du tentacule isolé de *Metridium*. Le nitrate de strychnine a donné le même résultat. Après l'addition de la drogue à l'eau de mer, en concentrations de 10^{-6}, 10^{-5}, et 10^{-4}, il ne s'est produit aucun changement du mouvement ciliaire. La nicotine et la strychnine lesquelles, dans les concentrations employées, ont une action marquée sur le système nerveux central et périphérique chez les animaux supérieurs, n'ont manifesté aucune influence sur les cils de *Metridium*. Ce fait est vraisemblement explicable par l'absence d'une innervation des cellules des cils vibratils, ce que Burn et ses collaborateurs supposent eux-aussi. Les hormones, adrénaline et acétylcholine, doivent avoir par conséquent une action directe sur la vibration ciliaire. Les résultats de nos recherches s'accordent bien, en ceci aussi, avec l'expérience acquise par Burn et ses collaborateurs.

RÉSULTATS DES EXPÉRIENCES

L'action de quelques substances pharmacologiques a été examinée quant à leur influence sur les mouvements des cils de petits tentacules isolés de *Metridium senile*. On a fait l'usage pour cela du déplacement de tentacules isolés, qui a lieu grâce à leur vibration ciliaire. Nous avons déterminé le temps nécessaire (sec.) au tentacule isolé pour parcourir 10 mm dans un petit appareil construit spécialement à cet effet.

Après la détermination de divers facteurs (tel que t° et pH) qui influencent la vitesse du mouvement des cils en eau de mer pure, nous avons examiné l'action de quelques substances pharmacologiques. Il a été démontré ainsi que l'adrénaline et l'acétylcholine ont, chez *Metridium*, une action différente et antagoniste sur la vitesse du mouvement ciliaire.

L'adrénaline et la noradrénaline ont une action accélératrice sur le mouvement des cils. Les résultats de nos expériences s'accordent en ceci avec ceux de l'étude de Burn et de ses collaborateurs, lesquels ont observé de même une accélération des vibrations ciliaires après l'adrénaline. Chez *Metridium*, la noradrénaline a de même une action accélératrice sur le mouvement des cils. Chez *Mytilus*, on n'a pas observé d'accélération de ce mouvement par cette drogue, selon Burn.

Nos expériences nous ont permis de plus de déterminer que l'acétylcholine exerce une action inhibitoire sur les mouvements des cils des tentacules isolés de *Metridium*. Selon Burn, chez *Mytilus*, l'acétylcholine a une influence accélératrice sur le mouvement ciliaire. Il y a donc une différence dans l'action de l'acétylcholine sur les cils de *Metridium* un Coelentéré, et ceux de *Mytilus*, un Lamellibranche.

Finalement, nous avons pu déterminer que la nicotine et la strychnine, substances agissant principalement sur les éléments nerveux, n'ont pas d'influence sur le mouvement des cils. Basés sur ces résultats, nous pouvons conclure que les hormones adrénaline et acétylcholine ont une action directe sur les cellules ciliaires de *Metridium*.

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ON THE DISTRIBUTION AND ECOLOGY OF LITTORINA OBTUSATA (L.) AND ITS SUBSPECIFIC UNITS

by

J. J. BARKMAN

(including results obtained by G. J. H. Ebbinge Wubben and J. Verwey)

(Zoological Station, Den Helder)

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I. INTRODUCTION

A. ACKNOWLEDGMENTS

These investigations were carried out during the summer of 1948 at the Zoological Station of the Netherlands' Zoological Society at Den Helder. I want to express my sincere gratitude to the director of this institute, Dr. J. Verwey, who suggested the problem to me and kindly helped me in several ways. I also wish to thank the members of the staff for their technical assistance and Mr. J. Spiekerman for the correction of the English text.

The work consisted of an experimental part carried out in the laboratory, and field work, which was done in 1948 near Den Helder, on the island of Texel and in N.W. Scotland, in the summer of 1949 in S. Brittany, in the summer of 1950 at Narvik, Norway, and in the summer of 1951 on the island of Schouwen (Netherlands).

In the summer of 1939 G. J. H. Ebbinge Wubben studied the same problem at Den Helder, approaching it from a somewhat different angle. He kindly permitted me to make use of his results laid down in an unpublished manuscript.

B. SCOPE OF RESEARCH AND PROBLEMS INVOLVED

Littorina obtusata (L.) is one of the few animals in the Netherlands whose distribution is strictly limited to the intertidal belts of stony sea shores. The principal aim of this investigation was to find out the causes of this phenomenon, in particular why the snail does not occur above or below the littoral belt.

Field observations soon showed that the presence of certain brown algae is a conditio sine qua non for the occurrence of *Littorina obtusata,* a fact which had already been stressed in the literature on the subject and also by Ebbinge Wubben, as I found out later. The algae are in their turn restricted to certain levels of the tidal zone. Consequently, the problem fell into two distinct parts, viz.:

1. the question what is the exact nature of the connection between the snail and these algae;
2. the question whether, apart from this connection, there also exists a direct relation of the animal to the abiotic environment of the tidal zone, and, if so, what is the nature of this relation.

My own research chiefly dealt with the first problem, whereas the second problem was particularly studied by Ebbinge Wubben, who also worked on the combined influence of the algae and the abiotic factors.

Since such a close relation exists between the occurrence of *Littorina obtusata* and certain brown algae it seemed useful to describe briefly the algal zonation in the regions that were studied. This has been done in the chapters of part III, since the algae mainly affect the *vertical* distribution of the snail.

Littorina obtusata comprises a number of more or less distinct varieties. The field investigations made clear that part of these varieties differ not only in a morphological, but also in an ecological respect. Experiments in the laboratory confirmed this view in respect of two varieties.

I also made observations with regard to the horizontal distribution of *Littorina obtusata*, the results of which will be set out first.

II. THE HORIZONTAL DISTRIBUTION AND ITS CAUSES

A. THE HORIZONTAL DISTRIBUTION

1. *The distribution of the species as a whole*

Littorina obtusata occurs on both sides of the North Atlantic up to the Arctic Ocean (S. Greenland, White Sea). It is an essentially northern species, which is not found farther south than Cape Cod (Mass., U.S.A.), the Straits of Gibraltar and the Azores (Dautzenberg and Fischer, 1914).

In the Mediterranean the species is mentioned from two localities only: Malaga and Corsica.

It is not found in the Baltic, except in its westernmost parts.

2. *The subspecies and their distribution*

The subspecies of *Littorina obtusata* have been dealt with by Dautzenberg and Fischer (1914). Both the eastern coasts of North America and the western coasts of Europe are inhabited by the subspecies *littoralis*. It gradually merges into the arctic subspecies *typica*, in N. America via the variety *palliata*, in N.W. Europe via the variety *compacta*, both considered to belong to the subspecies *littoralis* (see also Colman, 1932). Accordingly, animals of the European variety *compacta* become more numerous towards the North (see table II). Even in N. Scotland I found transitional forms between this variety and the subspecies *typica*. These forms (along with *typica* proper) are also present among material from Reykjavik, Iceland, in the National Museum of Natural History at Leiden. The transitional forms constitute a large part of the total *L. obtusata*-population at Narvik (table II), which is situated on the very borderline between the two subspecies. Characteristic *typica* are still scarce there.

The subspecies *littoralis* is to be found as far north as Labrador, Iceland and the Lofoten (Norway), the subspecies *typica* inhabits the coasts of Greenland, Iceland, northern Norway, N. Finland, N. Russia and probably also parts of N. Canada.

Unless otherwise stated this paper deals only with the subspecies *littoralis*.

3. *The varieties and their distribution*

It is well known that *Littorina obtusata* shows extreme variations in colour, and, to a less extent, in the shape of its shell.

Before discussing the distribution of the varieties, it is worth while to consider their taxonomical validity. Do they indeed represent true varieties or merely sex or age differences or phenotypical variations? In the following I shall restrict myself to the colour varieties.

The possibility of phenotypical variation may be excluded. According to Linke (1934) current velocity, salinity and illumination have no influence upon the colour of the shell in the genus *Littorina*. Other important habitat factors might be the food (i.e. the species of algae consumed) or the level within the tidal zone, on which depends a complex series of factors, such as desiccation, temperature, fresh water influence, and illumination. We can find nearly all colour varieties, however, in conjunction with every species of algae and at every level.

The possibility of sexual dimorphism must be rejected in view of the observations made by Pelseneer (1920). See also Linke (1934).

As to the third point, I think it quite possible and even probable that part of the varieties represent merely different age stages. This holds in particular for the variety *reticulata*, which I consider to be a juvenile stage of the variety *fusca* on account of the following facts:

1. The variety *reticulata* is generally smaller.
2. In growing *fusca* the youngest part of the last whirl is often reticulate.
3. I was able to make even plain brown individuals completely reticulate by removing the continuous brown outer conchyoline layer with the aid of hydrochloric acid. The latter assumed a brown colour then. Something similar occurs in nature, where in old individuals of the variety *fusca* the brown layer of the oldest whirl often wears away, thus revealing the reticulate pattern.

Further, the variety *inversicolor* probably always starts life as *albescens* or *citrina*, for in young specimens of *inversicolor* the dark bands are still very inconspicuous[1].

Finally, there is the question of the varieties *citrina* and *olivacea* and their relation. This is especially important since the experimental work was done with these two varieties.

First of all, it must be remarked that the green colour in *Littorina obtusata* is partly, sometimes even wholly, due to a cover of unicellular green algae, which can be removed by scratching them off or by boiling the shells in concentrated lye, which is then coloured green by the dissolving chlorophyll. These algae are sometimes present on the shells of *citrina* and they are then the only cause of the (bright) green colour. The algae seem to be invariably present on *olivacea*, but this variety also has an (olive) green colour which cannot be extracted by boiling lye, not even after application of hydrochloric acid which dissolves the outer shell layers. This colour must therefore be due to a pigment produced by the animal itself, and not to algae, endolithic species included.

One might be inclined to believe that the variety *citrina* represents a juvenile form of the variety *olivacea* in view of the following facts:

1. Specimens of *citrina* are generally smaller than those of *olivacea*.
2. Individuals of an intermediate colour, marbled yellow and green ones, and green animals with a yellow zone near the mouth, can all be found, whereas yellow specimens with a green growing zone do not occur.

Nevertheless, I am of opinion that *citrina* is a distinct, independent variety, since:

1. One will find big yellow specimens and small green ones.
2. The calcareous inner layer of the shell is white in *citrina*, dark violet in *olivacea*, which is visible on the parietal innerside of the mouth. It may also be seen on the outer surface of the shell, after removal of the conchyoline layer with acid.
3. The animals of the variety *citrina* are unpigmented and cream-coloured, those of the variety *olivacea* are highly pigmented and dark grey or black. Transitional forms between the two extremes do indeed exist, but they are far less frequent than those between the extremes of shell colour.
4. In several regions the variety *citrina* is the only one found. This holds, for instance, for the Marsdiep near Den Helder and—according to DAUTZENBERG and FISCHER—for parts of Normandy.

I am therefore inclined to believe that, though some of the "varieties" described possibly represent nothing but age stages, most of them must be regarded as true varieties.

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[1] This need not mean that every individual of *albescens* or *citrina* will develop into *inversicolor*, for we can find very old *citrina* individuals without any trace of dark bands. It does mean, however, that what we call *albescens* and *citrina* must represent heterogeneous units from a taxonomical point of view.

If, now, we turn our attention to the distribution (and ecology) of the varieties, we should first of all realize that the colour varieties are more important than the form varieties, since the latter show many transitions and are often difficult to distinguish, particularly when juvenile. Moreover, according to LINKE (1934), the so-called form varieties possibly represent nothing but different phenotypes. Finally, form and colour may vary independently in *Littorina obtusata*. We will therefore consider the colour varieties regardless of their form.[1]

The second point which must be stressed is that differences in distribution between the various varieties are mainly a matter of density. Now, the numbers of individuals found in a certain locality, partly depend upon the density of the algal cover, which shows considerable local variation. It is therefore more reliable to compare figures that give the percentages of the total number found in a given locality or habitat than numbers of individuals. This has been done in tables I and II.

LOCALITIES

On the island of Schouwen (Holland) one transect was studied, on the dike near the western end of the south shore, near Burgsluis. The localities near Den Helder (harbour and sea dike) and on the neighbouring island of Texel (E. coast near Oude Schild) are indicated in fig. 1. In N.W. Scotland four transects were studied, three near Lochinver (W. coast) and one near Bettyhill (N. coast), both situated in Sutherland (see fig. 2). In S. Brittany two localities were studied with one transect each, viz. the E. coast of the peninsula of Quibéron near St. Julien, and the S. coast of the peninsula of Pont l'Abbé (Quimper), South of Loctudy. In N. Norway one transect was studied, near Håkvik, S.W. of Narvik, on the S.shore of the Ofotfjorden; this firth is 5 km broad near Håkvik, but in places narrows to 3 km towards the sea.

Near Den Helder, on Texel and on Schouwen the shore is an artificial dike of basalt stones, in all other places a natural rocky shore, only in Brittany interrupted by sandy beaches, and stretches with sand behind and among the rocks. Near Narvik and at Lochinver B the water was slightly brackish, perhaps also near Bettyhill.

All observations were made at low tide and in summer, near Den Helder at the end of June, on Schouwen in the middle of September, in the other localities in the beginning of August.

On each alga species in each of the transects of the different localities 30 minutes' collecting was done, except in Narvik (15 min.) and Den Helder (time not noted). Since the number of transects studied and of algae present within each transect were not the same everywhere, the total time of collecting was different (Scotland 5 hours, Brittany 4 hours, Schouwen 2 hours, Narvik 1 hour). Table I gives the total numbers of animals collected in each region, and the numbers when reduced to 1 hour's collecting.

In order to get purely geographical data, habitat factors had to be eliminated as far as possible. For each locality the animals from all habitats (sheltered as well as exposed, from all different levels and algae) have therefore been taken together. In this way the shelter (exposure) factor was eliminated, except in the cases of Narvik and Schouwen, where only a single transect could be studied: one on a rather sheltered coast near Narvik, the other on a rather exposed shore on the island of Schouwen. The animals were always taken from the same set of 4 algae, viz. the 3 *Fucus* species and *Ascophyllum nodosum*. Therefore, the Scottish animals, collected on *Laminaria*, have not been taken into account, since no collecting was done on this kelp in the other places. In the Scottish transects not all of the 4 Fucaceae were always present. In this case a correction was made.

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[1] Transitions also occur, though more rarely, between various colour varieties. Besides, we may find combinations of colour patterns. To the combination *inversicolor-reticulata* mentioned by DAUTZENBERG and FISCHER I can add a combination *zonata-reticulata*.

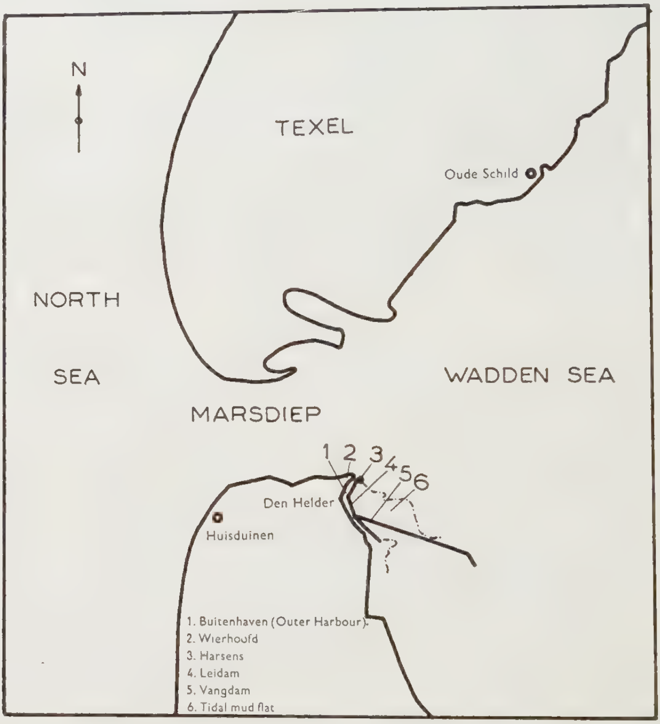

Fig. 1. Localities of observation near Den Helder and on the island of Texel.

In the early stages of the field work no distinction was made between var. *citrina* and var. *albescens* (see Dautzenberg and Fischer, 1925). The latter has therefore been included here in the former variety in all tables.

It follows from table 1 that variability in colour is greatest in S. Brittany and Scotland, smaller near Den Helder and particularly on the island of Schouwen. The absence of a few rare varieties from Narvik may be accidental and merely the result of a too small total number of animals collected there.

The variety *fusca* is undoubtedly most abundant in Scotland. The same applies to var. *ziczac*, which is atypical in Brittany. A distinctly northern distribution is only shown by var. *rhabdota*.

In spite of the very small percentage of var. *alternata* in S. Brittany, statistical calculations, for which my thanks are due to Dr. H. R. VAN DER VAART, proved that this variety has a significant preference for that coast. This does not apply to var. *rubens*.

Not too much value should, however, be attributed to the figures for var. *olivacea* and *citrina*, since their relative abundance varies much more within one region than between two different regions: for var. *olivacea* it varies from 11 to 58 % in Brittany, for var. *citrina* it varies between 25 and 55 % in this region, between 30 and 92 % near Den Helder and from 4 to 50 % in Scotland.

As to the form varieties, it is evident from table II that the variety *retusa* is most abundant in the South (Brittany, Schouwen) and becomes scarcer towards the North, but it is still recorded as far north as the Lofotes near Narvik (DAUTZENBERG and FISCHER, 1914). Statistical calculations proved that there is neither a significant difference between the percentages for Brittany and Schouwen nor between those for Den Helder and Scotland, but the variety is decidedly more abundant in the former two regions than in the latter two and more so in the latter than at Narvik. We must bear in mind, however, that the form varieties are perhaps nothing but phenotypes, in which case this observation would mean that a warmer climate favours the development of a *retusa* modification.

B. THE CAUSES OF THE HORIZONTAL DISTRIBUTION

1. *Abiotic factors*

a. *Temperature*. There is little doubt that the existence of well defined southern limits of the species as a whole must, as in so many other species, chiefly be accounted for as a matter of temperatures. Perhaps the same is true of its northern limits.

Both in N. America and in Europe the distribution of the snail extends southwards to a point where a steep upward gradient of the sea temperature is observed. In the U.S.A. the southern limit is to be found near Cape Cod, an important zoogeographical barrier for many marine animals. Here the cold Labrador and the warm Florida currents meet (FLATTELY and WALTON, 1922; JOHNSON and SKUTCH, 1928; DEXTER, 1947). The average temperature for July at Cape Cod is 20° Celsius. In Europe the southern limit lies near Gibraltar, where the average temperature of the surface water in the warmest month of the year (August) is 21° C, which suddenly becomes 24° as soon as we enter the Mediterranean. It therefore seems probable that the summer temperature determines the southern limit of the species. Of course, what we ought to know are the maximum day temperatures to which the surface of the algae on which *Littorina obtusata* lives, may be exposed during low tide. These temperatures are not known, but they will certainly be higher than those of the sea water. Lethal maximum temperatures might therefore account very well for the southern limit. According to HAYES (1929) adult animals become inactive at 25°, while eggs are stated to die at 26° C.

In America the problem of the southern limit is less complicated than in Eurafrica: south of Cape Cod the shore is continuous and inhabited by *Ascophyllum nodosum* as far south as New Jersey, by *Fucus vesiculosus* even as far as North Carolina. East of Gibraltar not only is the temperature much higher, but *Fucus* and *Ascophyllum* are absent too. South of Gibraltar, on the Atlantic coast of Morocco, where the snail is absent, *Fucus spiralis* and *vesiculosus* are found, often forming dense vegetations. What is more, the temperature of the sea water does not exceed 18° C in many places. Perhaps the Straits of Gibraltar are in the nature of a geographical barrier to the snail, but in view of its total area of distribution, in which much larger geographical disjunctions are found, this hardly seems probable. Dr. J. FURNESTIN, Director of the Zoological Station at Casablanca, suggests in a letter to me that the Straits of Gibraltar might represent a thermal barrier, since a superficial sea current of more than 22° C enters these Straits from the Atlantic. But the barrier only exists in summer. I consider it more likely that the maximum air temperature is the limiting factor here[1].

Though *L. obtusata* is found in Greenland, it is absent from the northern parts, e.g. from the bay of Upernavik on the N.W. coast, although this bay is sheltered and *Fucus* is still present even in the intertidal belt (MADSEN, 1940). Probably the temperature is responsible for the absence of the snail. Since *L. obtusata* can stand temperatures of minus 30°C, even for a long period (DEXTER, 1947), it seems probable that it is not the low winter temperatures which constitute the limiting factor here, but the low summer ones, preventing the snail from spawning.

It is, however, quite possible that in the Arctic Ocean the low salinity especially of the surface layers near the coast (melting ice) also forms an important factor, since *L. obtusata* is very sensitive to low salinities (see below).

b. *Salinity*. The species does not occur in the Baltic east of the Neustadter Bucht (Germany) and Landskrona (Sweden). Since one of the algae, vital to its existence, viz. *Fucus vesiculosus*, penetrates into the Baltic even up to the Gulf of Finland (Segerstråle, 1928, 1944), it can hardly be doubted that low salinity is the limiting factor here. The average surface-salinity near Neustadt-Landskrona is about $15\,^{0}/_{00}$ in February, about $12\,^{0}/_{00}$ in June[1]. The lack of tides cannot be essential, see below. The snail was also absent from the former Zuiderzee south of the island of Wieringen, though *Fucus* was found there. According to Verwey (verbal communication) the average salinity was about $22\,^{0}/_{00}$ there, but variations were considerable, ranging from something like 12 to $28\,^{0}/_{00}$. According to Ebbinge Wubben the species occurs throughout the rather salt Eastern Scheldt (average salinity about $28\,^{0}/_{00}$), but in the brackish Western Scheldt it has been found up to Hansweert only. In Scotland I was able to establish that the snail is absent from brackish estuaries. In literature too, its absence from estuaries (N. America) is reported (see Hasemann).

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[1] The lethal temperature seems to be much lower when the animals are exposed to the air (snails inactive at 25° C.) than in case of submergence (higher than 42°, according to GOWANLOCH and HAYES, 1926; the data of these authors seem not to be very reliable, however).

The species is very sensitive to fresh water (Colgan 1910, and Pearse 1929). Experiments made by Hertling (1928) showed that the development of the eggs ceases at or below $25\,^{0}/_{00}$ total salinity. Animals from water with high salinities soon die in water of about $15\,^{0}/_{00}$. But from the data mentioned above it will be evident that the species can stand somewhat lower salinities in nature.

Ebbinge Wubben already pointed out that the animals living within brackish habitats may be more tolerant to low salinities than those living on open sea shores. They have probably grown adapted to low salinities in the long run, a phenomenon to be met with in many organisms.

c. *Watermovement.* The magnitude of the tidal amplitude does not seem to influence the occurrence of *Littorina obtusata*. It is even found in places where the tides are practically nil (Gullmar Fjord in W. Sweden). Its absence from the Baltic and the greater part of the Mediterranean is due to other factors (see pp. 29–31 and 35–36).

Neither does the species appear to be affected by strong tidal currents, provided they do not entirely remove the algae on which it depends: in Brittany, according to Fischer, the snail is found in tidal channels with current velocities up to 17 km an hour.

Strong surf, however, cannot be tolerated. Special attention has been given to the influence of surf during the observations in the field. In Brittany, Den Helder, and Scotland, stations with various degrees of shelter and exposure were examined, the most complete series being the Scottish one.

[1] According to Ökland (1933) *L. obtusata* is found near Tromö in the Skagerrak (Denmark) in water with a salinity ranging from 10 to $15\,^{0}/_{00}$.

In Brittany the eastcoast of Quibéron is slightly more sheltered than the S. coast near Kergoff (Pont l'Abbé). Near Den Helder the surf gradually increases as one moves away from the harbour towards the open sea (Huisduinen) (fig. 1). In Scotland the intensity of the surf increases in the sequence Bettyhill, Lochinver B (very small, N. exposed bay), Lochinver C (very small, S. exposed bay) and Lochinver D (Kirkaig Point, extreme W.) (fig. 2).

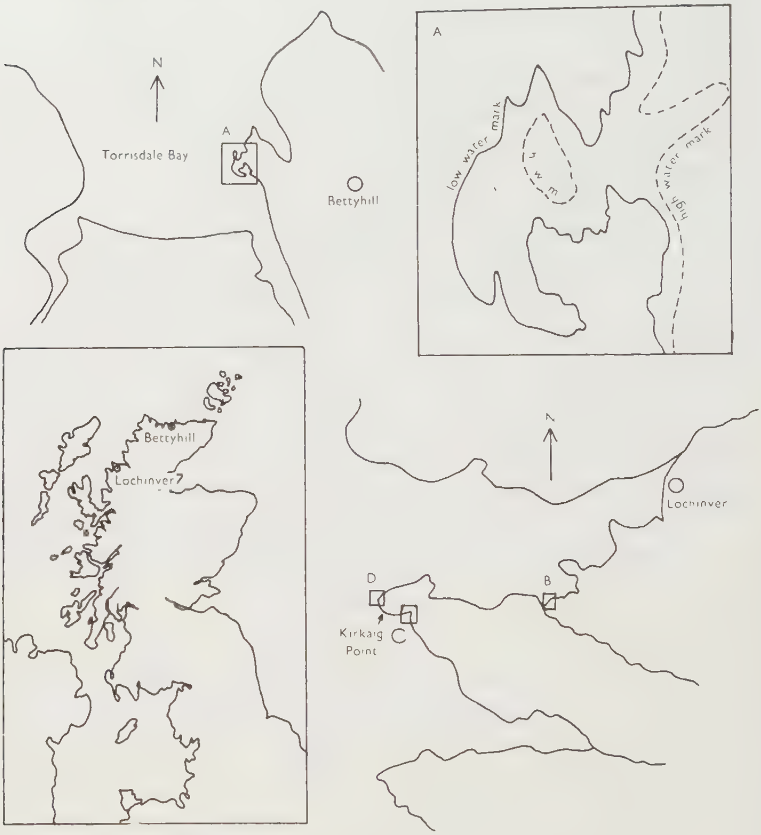

Fig. 2. Areas investigated in N. Scotland.

That strong surf cannot be endured is proved by the fact that the species is absent from surf-beaten coasts, even where Fucaceae are still present, for instance on the massive piers of IJmuiden and Hook of Holland and on the North sea dike from Camperduin to Petten (Holland), where there is no sand to interfere with them. The snail is also absent from all smaller breakwaters along the sand beach of the Dutch coast; these are partly covered with Fucaceae, but here the sand from the shore immediately around might be an adverse influence.

Surf may affect the animals directly, but also indirectly, through the algae, which are likewise influenced by the surf.

The direct influence of surf appears to be a complicated one. The lower limit of the vertical range on the shore shifts to higher levels (both in *L. obtusata* and *L. littorea*) when we go from sheltered to surf-beaten stations. In the harbour of Den Helder, where there is no surf at all, the range of *L. obtusata* extends downward to just below M.L.W.S., thus including the *Fucus serratus*-belt. Along the Marsdiep the lower limit rises with increasing surf towards the open North Sea. Consequently, the lowermost zone (that of *Fucus serratus*) does not contain *L. obtusata* along the western part of the dike. The variety *olivacea*, being the more sensitive to surf action of the two varieties present near Den Helder, is wholly absent here, whereas the variety *citrina*, which otherwise has a strong preference for *Fucus serratus*, is confined to the higher growing *Fucus vesiculosus* for which it has a less pronounced liking. For these reasons the species as a whole is much less abundant there. Still farther West, where the dike faces the North Sea, the variety *citrina* (and so the whole species) is completely absent, though Fucaceae are still present.

As stated above, the animals are also affected by surf through the algae. Increasing surf causes the algae to disappear, one species after another. Now, the sequence, in which the Fucaceae disappear, is not the same in all places. In Brittany[1], *Fucus serratus* is the last to disappear, but where surf is so strong that only this kelp is left, this very surf makes life at the *Fucus serratus*-level impossible to *L. obtusata*. Consequently, the snail is absent from the shore there. But where *Fucus vesiculosus* is the most surf resistant alga, as in N.W. Scotland, *L. obtusata* may still be present in places where only this alga is left (table x).

The influence of surf on the distribution of the varieties is evident from tables IV and XI. In order to eliminate the specific influence of the algae I have summarized in table XII the numbers of animals found on *Fucus vesiculosus*, the only alga species that is found on all the shores, from the most sheltered to the most exposed, of the Scotland series, which is the most complete one.

It follows from the tables that not all *obtusata*-varieties show the same degree of surf tolerance. The varieties *olivacea* and *fusca* are most abundant on sheltered coasts, though *fusca* is still rather plentiful on strongly exposed shores in Scotland and even seems to prefer a slightly exposed habitat in Brittany. The variety *olivacea* shows the same distribution in Brittany and Den Helder as in Scotland: near Den

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[1] The same situation is encountered on the so called Wierhoofd near Den Helder.

Helder its frequency along the exposed Marsdiep is 0–2 %, in the northern part of the harbour about 15 %, in the southern part about 40 % of the total population.

Var. *inversicolor* prefers a somewhat less sheltered habitat, and the varieties *citrina* and *ziczac* are mainly found in moderately exposed stations. Of var. *citrina* this is also true in Brittany and near Den Helder.

If we compare these statements with the preference of the varieties for the various algae and with the influence of surf intensity upon these algae, we can find out to what extent each variety is really "surf-loving" or "surf-tolerant", or how far this is only apparent and due to the influence of surf on its favourite alga species. Finally, we can check the result thus obtained by comparing it with table XII (behaviour of the varieties in different surf intensities on one and the same alga species).

Example: Var. *citrina* is most abundant on shores with medium surf intensity (table XI). So we are confronted with two problems: 1. Why is it less abundant on more sheltered shores? 2. Why is it less abundant on strongly exposed shores? From table XV it is evident that var. *citrina* prefers *Fucus serratus*. This alga is found on the most sheltered shores (Bettyhill, table X); so we may conclude that absence of surf seems to influence "directly" (at any rate not through the algae) the abundance of this variety. On strongly exposed shores (Lochinver, W. point; table X) *F. serratus* is not found however. Consequently, this fact no doubt partly accounts for the reduced density of the variety *citrina* there, since the other alga present *(F. vesiculosus)* is less frequented by the snail on all types of shores. But here, too, the existence of an (additional) "direct" surf influence cannot be denied, for it appears from table XII, that even on the same alga *(Fucus vesiculosus)* the abundance of var. *citrina* decreases towards the open sea.

Hence, considering only "direct" surf influence, we may probably conclude that the varieties *fusca*, *olivacea*, and *inversicolor* are not or hardly surf resistant, whereas the variety *citrina* is able to stand some surf. It is further probable that the varieties *citrina*, *inversicolor*, and *ziczac* do not thrive where surf is weak. Of course, this may be due to other influences and not to the absence of surf as such, but at any rate it is not due to the algae.

As to the form varieties, it is evident from table XIII that they are increasingly surf-loving in this sequence: *compacta*, *retusa*, *pachychila*, *vittata*, and it follows from table XIV, that, as far as var. *compacta* and *vittata* are concerned, this is a "direct" effect of the surf. But according to LINKE (1934) watermovement has a strong influence upon the shape of the shell in the genus *Littorina*. If this is also true of *L. obtusata* (but it is somewhat contradicted by the fact that nearly all varieties were found in various states of exposure), this would of course mean that in quiet water the shells develop into *compacta* and *retusa* forms, in heavy surf into *pachychila* and *vittata* forms. It is remarkable that on strongly exposed shores the individuals of all "varieties" remain very small and develop very thin and brittle shells.

d. *Substratum and suspended matter. Littorina obtusata* lives on the fronds of large sea-weeds. Substratum and suspended matter therefore may indirectly affect the distribution of the snail by affecting these algae, causing them to disappear. A direct influence of the substratum is only possible where surf is so strong that the animals are detached from the algae, a direct influence of suspended matter is only to be met with where the water is so quiet that the suspended particles are deposited on the algae and animals.

As to the direct influence of the substratum, we have seen that *L. obtusata* is absent from the surf-beaten piers along the sand beach of the Dutch coast. This might be due to surf action alone, but probably the presence of sand also has an adverse influence, not only on account of its scoring action, but also because animals that are detached from the algae and fall on to the sand, appear to be lost. In the laboratory I observed that the snails can hardly move on sand, and when trying to do so, the entrance of their shells is filled with sand and the animals are soon suffocated. Where surf is weak, however, so that the animals are not detached from the sea-weeds, the snail can live in the presence of sand: in S. Brittany I found it on algae attached to boulders which were scattered over a sand beach in a sheltered bay. Yet, many dead animals were found on the sand.

As to the direct influence of suspended matter, algae and animals are continually covered by it in places where the seawater contains large quantities. Where currents are strong, this silt is readily removed, but in quiet water the whole substratum is smothered. This probably accounts for the fact that we do not find the snail on the stony dike in the muddy southern part of the harbour of Den Helder, nor on tidal mud flats, although *Fucus* is present in both cases.

2. *Biotic relations*

Only the relation between *L. obtusata* and the Fucaceae on which it depends will be discussed in this paper. This relation is of primary interest with regard to the vertical distribution of the snail and will consequently be dealt with in more detail in part III. It is, however, also of interest in connection with the horizontal distribution of the snail, since the latter can not live in regions where Fucaceae are absent. The absence of *L. obtusata* from these regions is, however, generally due to abiotic factors, influencing directly both snail and sea-weeds. In a few cases only its absence seems to be caused by the absence of Fucaceae, e.g. in places where these algae have been removed by the scouring effect of floating ice or by man.

L. obtusata has been reported from two localities in the Mediterranean, viz. Malaga and Corsica. In the whole western part of this sea *Fucus* and *Ascophyllum* are absent, the only Fucaceae found there being *Sargassum* and *Cystoseira*. The species of both genera live in the sublittoral belt. Only *Cystoseira mediterranea* reaches low water mark and might therefore be suitable for our *Littorina*. As this alga is widespread along all coasts of the Mediterranean, it is hardly understandable why *L. obtusata* should be limited to Malaga and Corsica and be absent from the cooler coasts of S. France. I therefore doubt the correctness of the record concerning Corsica. As to Malaga, it might very well be that the *Littorina* found here was cast ashore along with algae from the Atlantic. From this very locality there are reports of atlantic algae, a.o. *Fucus axillaris*, having been cast ashore. This *Fucus*, closely related to *Fucus vesiculosus*, grows W. of Gibraltar and is probably the species on which *L. obtusata* lives in S.W. Spain. We may therefore assume that *L. obtusata* is absent from the whole Mediterranean.

Only one *Fucus* species is indigenous in the Mediterranean. This is *Fucus virsoides*, which is closely related to *Fucus spiralis;* it is limited to the Adriatic Sea. The absence of *L. obtusata* from this sea may be due to a lack of accessibility or to unfavourably high temperatures, for even in the northernmost part of this sea the average temperature of the surface water in August is 24 C°, which is too high for the snail (see p. 29).

Our conclusion is that the absence of *L. obtusata* from the whole Mediterranean basin may be explained as being due to high temperatures and lack of accessibility, except perhaps for the cooler coasts of S. France where the absence of suitable Fucaceae might be responsible. The influence of these algae on the horizontal distribution of the snail therefore appears to be very slight and of a merely local character.

3. *Geographical and historical factors*

The tropical regions with their high temperatures and practically no littoral vegetation undoubtedly constitute an effective barrier to the spreading of *L. obtusata*. This might be the reason why the species does not occur in the temperate zones of the S. Atlantic. As it appears that *Fucus* and *Ascophyllum* are not found there, there is no conclusive evidence that the absence of the snail must indeed be attributed to the effectiveness of the barrier.

In the N. Pacific, however, sheltered rocky coasts with clear, salt water, a broad tidal zone and a *Fucus* vegetation are to be found in many regions which also have a suitable climate. Here, the absence of *L. obtusata* is beyond doubt due to historical factors (it either had its origins elsewhere or it was extinguished in the Pacific during a warmer climatic period) and to geographical factors (lack of accessibility).

4. *Conclusions*

The horizontal distribution of *Littorina obtusata* appears to be due first of all to geographical and historical factors, which limit its area to the N. Atlantic, and secondly to temperature, limiting the area to the temperate and cold parts of this Ocean. Within this region again, the distribution is further narrowed down by sea water salinities below 10–15 $^0/_{00}$. Lastly, local occurrence is determined both by salinity and by more or less heavy surf, a sandy substratum, high silt concentrations in relatively quiet water and the local distribution of *Fucus* and *Ascophyllum*.

As regards the varieties, we find that their distribution, in particular the area of their greatest density, may vary somewhat, apparently under the influence of temperature and, as far as their local occurrence is concerned, under the influence of surf.

III. THE VERTICAL DISTRIBUTION AND ITS CAUSES

A. THE VERTICAL DISTRIBUTION

From a biological point of view it would serve no useful purpose to express the vertical range of a species inhabiting the tidal zone in terms of absolute height above or below mean sea level. It has therefore been described here in terms relative to tidal levels and to algal zones.

1. *The distribution in relation to tidal levels*

a. *The tidal levels.* It is customary to denote tidal levels by initials. For readers not acquainted with them a short explanation is given here.

Mean sea level is indicated by M.S.L., mean high and low water mark by M.H.W. and M.L.W. respectively. Every fortnight there is a spring tide, in which the tidal amplitude is larger (high water is higher, low water is lower) than normal, in between there is a neap tide with an abnormally small tidal amplitude. We therefore distinguish high and low water spring tide (H.W.S. and L.W.S.) and high and low water neap tide (H.W.N. and L.W.N.). Since the levels of these spring and neap tides vary according to the season, a distinction is made between mean and extreme values (for instance M.H.W.S. and E.H.W.S.). The extremes occur only once or twice a year. Except when otherwise stated, the indication "extreme" always refers to the *highest* high water spring and low water neap marks, and to the *lowest* high water neap and low water spring marks. On each tidal shore we can therefore distinguish the following tidal marks, in a downward direction:

E.H.W.S., M.H.W.S., M.H.W., M.H.W.N., E.H.W.N., M.S.L., E.L.W.N., M.L.W.N., M.L.W., M.L.W.S., E.L.W.S.

As a rule, the other tidal marks are not indicated.

b. *The distribution of the species as a whole in relation to tidal levels.* According to Moore (1940) the upper limit of *Littorina obtusata* varies between just above M.H.W.N. and M.S.L. (sporadically near M.H.W.S.). According to Colman (1933 and 1940) the upper limit is found at E.H.W.N. or at M.H.W. These data refer to England. Gislen (1930) mentions M.S.L. for W. Sweden, and Dexter (1947) found the upper limit just above E.H.W.N. for Massachusetts, U.S.A.

The lower limit is given by Moore as E.L.W.S. (not abundant below M.L.W.S.), by Colman (1940) and Gislen as halfway between M.L.W.S. and E.L.W.S. (far from abundant below M.L.W.N.). According to Dexter it lies halfway between M.L.W. and M.L.W.S.

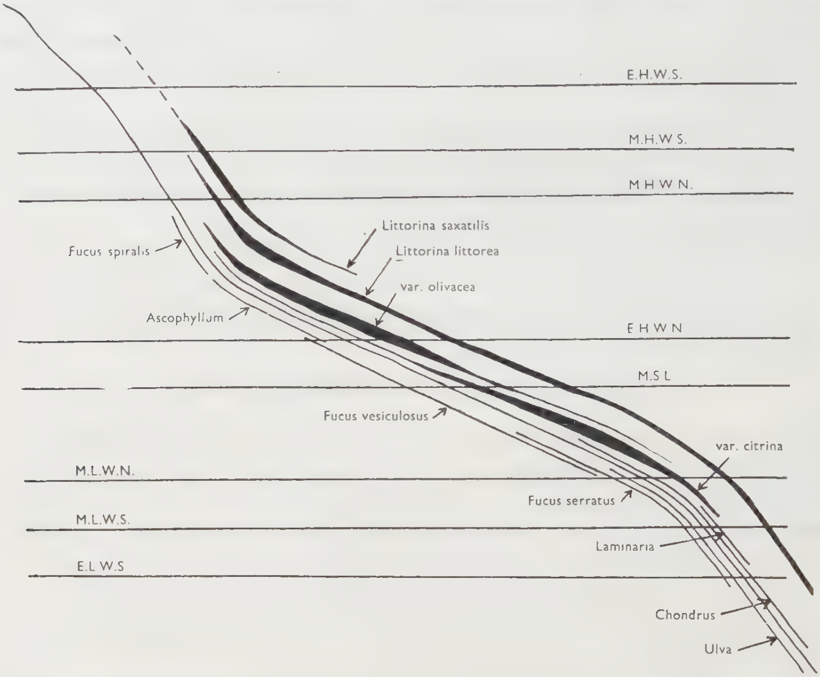

Fig. 3. Schematic representation of algal and *Littorina* zonation near Den Helder. For an explanation of tidal levels see text.

We may therefore assume that the mean upper limit lies at M.H.W.N., the mean lower limit halfway between M.L.W.S. and E.L.W.S. According to these data the extreme range extends from just below M.H.W.S. down to E.L.W.S. The optimum level has been identified as coincident with M.S.L. (Colman, 1940).

From my own observations I found that the upper limit lay around M.H.W. in most regions I visited. In Scotland and Schouwen it was found to be slightly higher on account of the occurrence of the snail on *Pelvetia*, which was not inhabited near Narvik and in S. Brittany. Near

Den Helder the upper limit lay lower, at M.H.W.N. *Pelvetia* is absent there and *Fucus spiralis* is reaching less high.

The lower limit of the species and the optimum level of the subspecies *littoralis* show a downward trend from the South towards the North. In S. Brittany the lower limit lies at M.L.W.S., at Den Helder slightly below M.L.W.S , in N. Scotland below E.L.W.S. The exceptionally high lower limit at Narvik (E.L.W.N.?) will be discussed below (p. 42).

The optimum ranges in the different regions will be evident from fig. 5.

These facts show that *Littorina obtusata* is able to live in habitats which are subject to fortnightly immersions only, as well as in places which fall dry but once every six months. According to COLMAN (1933) the time of exposure to the air of its normal habitat ranges from 65 to 5% in S. England. This does not necessarily imply that the animals are subjected to the same exposure percentages, for up and downward migrations probably occur.

c. *The distribution of the varieties in relation to tidal levels.* The upper and lower limits of the varieties have rarely been determined directly in relation to tidal levels or to exposure percentages. At Den Helder EBBINGE WUBBEN and I determined in which algal zones the var. *citrina* and *olivacea* are found. From these observations EBBINGE WUBBEN calculated their exposure percentages. This was possible because ZANEVELD (1937) published the exact exposure percentages of the littoral algae near Den Helder. EBBINGE WUBBEN found an exposure range from 0 to 46% for var. *citrina*, and from 30 to 80% for var. *olivacea*.

2. *The distribution in relation to algal zonation*

As stated before (see p. 35) *L. obtusata* is only found where Fucaceae occur. These form different zones within the tidal belt. It is therefore worth while to consider the relation between the vertical distribution of the snail and that of the algae in detail. Before dealing with this relation, it will be necessary to give a survey of the algal zones.

a. *The zonation of the algae.* The zonation of the algae near Den Helder has been thoroughly investigated and mapped by ZANEVELD (1937). He studied the distribution of *Ascophyllum nodosum* and the three *Fucus* species *(spiralis, vesiculosus, serratus)* in the harbour (which at that time was in effect a tidal creek about 1 km long). I myself studied the vertical distribution near Den Helder, on the islands of Texel and Schouwen, in some places in S. Brittany, in N. Scotland and near Narvik. My observations included other brown kelps and the large red and green algae. No exact determinations of tidal levels were made, as was done by Zaneveld. Zonation studies in adjacent regions have been made on the islands of Ré and Yeu off the S. coast of Brittany (Beauchamp, 1923), on the N. coast of Brittany (Fischer, 1929), in S.W. Scotland King and Russell, 1909; Flattely and Walton, 1922; Kitching, 1936), on Clare Island off the Irish West coast (Cotton, 1912) and on the Faeroer (Börgesen, 1908).

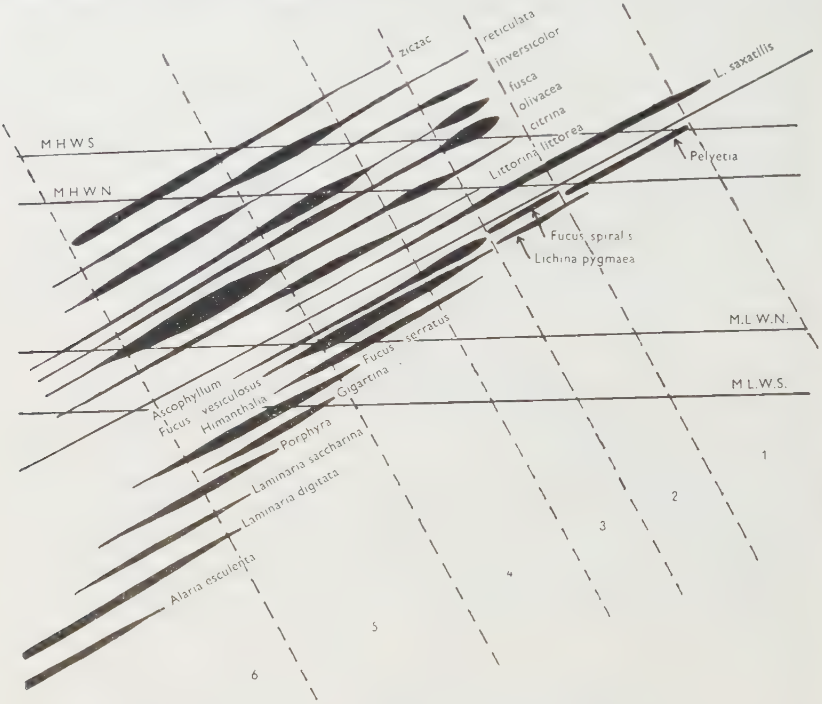

Fig 4. Schematic representation of algal and *Littorina* zonation in N. Scotland. For an explanation of tidal levels see text; 1–6 correspond to the algal belts, described on p. 40.

From all these data the following general zonation scheme (in downward order from high to low water mark) can be derived (see fig. 4):

1. A narrow belt of *Pelvetia canaliculata* between M.H.W.S. and M.H.W.N., sharply separated from:
2. A somewhat broader belt of *Fucus spiralis*, fairly well marked off from:
3. A still broader belt of *Ascophyllum nodosum* down to E.H.W.N., often with scattered *Fucus vesiculosus*. This belt rather gradually passes into:

4. A broad belt of *Fucus vesiculosus* around M.S.L., with scattered *Ascophyllum* in the upper half and scattered *Fucus serratus* in the lower portion. Near Den Helder *F. vesiculosus*, according to ZANEVELD, reaches downwards to M.L.W.N. or even to M.L.W.S.
5. A rather broad belt of mainly *Fucus serratus* and *Chondrus crispus*, gradually merging into:
6. A belt of *Laminaria digitata*, *L. saccharina*, *Alaria esculenta*, *Halidrys siliquosa*, *Porphyra laciniata*, and *Ulva lactuca*. This belt is mainly sublittoral and only its upper part falls dry at low water spring tide.

In Brittany and Scotland we find *Lichina pygmaea;* in Scotland this lichen is confined to belt 2, in S. Brittany it reaches upwards to above belt 1. At Den Helder *Pelvetia* is absent. In Scotland belts 3 and 4 sometimes intermingle completely, or even change places, *Ascophyllum* growing below *Fucus vesiculosus*, scattered between *Fucus serratus*. At Narvik, too, *Ascophyllum* grows at a lower level than *Fucus vesiculosus*, but here it forms a distinct belt, intercalated between the belts of *F. vesiculosus* and *serratus*. Near Den Helder *Gigartina stellata* occurs mainly in belt 3, in Scotland in belt 5. In Scotland *Fucus vesiculosus* is sometimes accompanied or replaced by *Himanthalia lorea*. In Brittany belt 5 also contains *Chorda filum*, belt 6 contains *Saccorhiza bulbosa; Alaria* and *Halidrys* were not seen there. At Narvik the *Laminaria* belt is replaced by a belt of *Furcellaria fastigiata*. Near Den Helder belt 6 is but very poorly developed and consists mainly of *Ulva*, *Porphyra* and *Chondrus*, while *Laminaria digitata* is confined to a few places.

b. *The distribution of the species as a whole in relation to algal zones.* In order to obtain comparable data, snails were collected in all regions for 30 minutes per alga species, except at Narvik (15 minutes). Therefore, the numbers of individuals have been doubled in tables XVII and XVIII. This method is somewhat arbitrary, but other methods met with great technical difficulties. Owing to the local absence of certain algae the numbers of snails on *Laminaria saccharina* and *Ascophyllum nodosum* in Scotland (table X) are based on only one survey of 30 minutes each, those for *Fucus spiralis* on two surveys, for *F. serratus* on three and for *F. vesiculosus* on four.

Therefore, the average number per locality (i.e. per 30 min. collecting) has been given in table X ,whereas the numbers in tables XV and XVI relate to a total of three surveys (90 min.) for each alga and each variety of *Littorina obtusata*.

The localities have been indicated on p. 27.

It follows from my observations that in S. Brittany (table III) the blunt periwinkle is most abundant on *F. spiralis* and that *F. vesiculosus* comes next.

On the island of Schouwen (table VIII) it is most abundant on *Fucus serratus*, near Den Helder on *F. vesiculosus*, in places on *Ascophyllum*, whereas *F. spiralis* is frequented least of all.[1] *Chondrus crispus* is the only alga besides *Fucus* and *Ascophyllum* on which *L. obtusata* has been found near Den Helder. On this species the snail is, however, very rare and only represented by the variety *citrina*.

In Scotland (table X) *F. vesiculosus* is the most frequented species. It is followed by *F. serratus* and *spiralis*, next comes *Ascophyllum*, finally *Laminaria saccharina*. A few animals were found on *Pelvetia* (on Schouwen too), none on *Himanthalia lorea*, *Laminaria digitata*, *Alaria esculenta*, *Halidrys siliquosa*, or on the green and red algae.

Near Narvik (table XVIII) the most striking fact is the almost entire absence of the snail on *F. serratus*. Possibly the animals had migrated to higher levels when I was working there. At the time *F. serratus* remained continuously immersed for a couple of days on end, which was not the case in the other localities. It should be remarked, however, that also at Quibéron (table III) the snail was far from abundant on *F. serratus*.[2] Another possibility might be that at Narvik the snail avoids the lowest level, because there is a more prolonged contact with brackish water, which is not liked by the snail, at this than at higher levels. Near Narvik *Littorina obtusata* does not show a clear preference for any of the other Fucaceae. However, if we consider only the subspecies *littoralis* (which is the only one present in the other regions), we find that the numbers at Narvik appear to decrease in the sequence *Ascophyllum* – *F. vesiculosus* – *F. spiralis*, in other words, according as the level is higher. The snails living there on *F. spiralis* were all found to be very small and to have thin shells. The same was the case with the snails from *F. vesiculosus* on the most exposed shores in Scotland.

Data on the occurrence of *L. obtusata* in relation to algal levels have also been given by TATTERSALL (1920) for Ireland, COLMAN (1940) for S. England, KING and RUSSELL (1909) and FLATTELY and WALTON (1922) for S.W. Scotland, GISLEN (1930) for W. Sweden, GOWANLOCH and HAYES (1926) for the E. coast of Canada, and DEXTER (1947) for Massachusetts. These records all present the same picture: that *L.*

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[1] This may be due to its minor density, for where it grows in dense patches the snail is sometimes numerous on this alga as well. On all the algal species the numbers of snails increase with increasing density of the algae. This corresponds with observations made by DEXTER (1947), who found the greatest abundance where *F. vesiculosus* and *Ascophyllum* had their greatest density. Presumably, a thick algal cover offers better shelter against desiccation and rain than a thin one.

[2] It has been stated that in S.W. Scotland (KING and RUSSELL, 1909) and W. Sweden (GISLEN, 1930) the snail is not even found on *F. serratus*! The data of KING and RUSSELL seem hardly reliable. In W. Sweden the explanation might be that *F. serratus* is permanently immersed there.

obtusata is restricted to the intertidal belt and that its numbers on different algae may vary according to the localities. In S. Scotland, according to KING and RUSSELL (1909), the snail seems to be most abundant on *Laminaria digitata(!)* and also present on *Ascophyllum* and *Fucus spiralis*, whereas no animals were observed on *Fucus serratus*, *Pelvetia*, and *Chondrus*. But FLATTELY and WALTON (1922), who studied the same region, did record the snail on *Fucus serratus!* In N.W. Scotland and Den Helder the species is not found at all on *Laminaria digitata*, but it is numerous on *F. serratus*. The data of KING and RUSSELL therefore seem hardly reliable.

Quantitative information has only be published by COLMAN (1940) and GISLEN (1930). They determined the numbers of each animal species found per kg of alga. GISLEN also indicated the numbers per square metre of rock surface. Since COLMAN also gave the weight of each alga species per sq.m., the numbers of animals per sq.m. can be calculated for S. England as well; they are given in table XIX. The figures given in that table under the heading: "Per sq.m." refer to the zones characterized by the particular algae mentioned. Animals found in that zone on other algae than the one mentioned have simply been added to those collected on the latter: the snails found on *Gigartina*, for example, have been added to those found on *Fucus serratus*. The numbers found on *Lichina* have been added both to those on *Ascophyllum* and to those on *F. spiralis*, since in that region *Lichina* forms a layer under both of them.

In W. Sweden *L. obtusata* is found almost exclusively on *F. vesiculosus*, *F. spiralis*, and *Ascophyllum*, sporadically on *Ulva*, *Enteromorpha*, and *Corallina*. There is a distinct preference for *F. vesiculosus*, both per kg of alga and per sq.m. of rock surface. This is evident from table XX, which I have compiled from GISLEN's work.

In S. England *Lichina pygmaea* is preferred to all Fucaceae! COLMAN, the only author who studied seasonal variation in the density of *L. obtusata*-populations, found, however, that the numbers on *Lichina* greatly vary with the seasons, whereas those on the algae are rather constant. On *Lichina* he found 400 snails per kg of lichen in September, 1650 in January and 4210 in March. This would suggest that the snail hatches on *Lichina*, after which the surviving juvenile animals migrate to the algae. This is corroborated by the fact that in S. England *Littorina obtusata* hatches in February and March[1] (in Holland this takes place in summer). Its density on *Lichina* is followed closely by that on *Ascophyllum*. It is much less on *F. vesiculosus*, while only few animals were found on *F. serratus* and *spiralis*, and none on *Pelvetia*.

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[1] Marine Biological Association: Plymouth Marine Fauna, 1931, p. 255.

Summarizing the facts, known from the literature and our own observations, we may state that:

1. *Littorina obtusata* nearly always has a distinct preference for *Fucus* and *Ascophyllum*. Exceptions are its abundance on *Lichina pygmaea* and *Zostera* (see below) in England and on *Laminaria digitata* in S.W. Scotland. The species has further been found on *Laminaria saccharina*, and—in very small numbers—on *Pelvetia*, *Chondrus*, *Ulva*, *Enteromorpha*, and *Corallina*.
2. The species generally prefers *Fucus vesiculosus* (E. Canada, N.W. Scotland, W. Sweden, Den Helder), sometimes *Ascophyllum* (S. England, a few localities near Den Helder, ssp. *littoralis* near Narvik), sometimes *Fucus spiralis* (S. Brittany) or *Fucus serratus* (island of Schouwen).

c. *The distribution of the varieties in relation to algal zones*. Very few observations have been made on this subject. A few remarks have been given by SLOFF (1925) and WRIGHT (1936). According to the former, var. *citrina* mainly occurs on *F. vesiculosus* in the Oosterschelde (Holland), var. *olivacea* (erroneously called var. *fusca* by the author) on stones above the algal zones and on *Ascophyllum*. According to WRIGHT, various colour varieties may be found on rocky coasts in England, but on *Zostera* mudflats only the "uniform dark greenish brown variety".

The results of my own observations are given in tables VI and VII for Brittany, in table VIII for Schouwen, in fig. 3 for Den Helder, in fig. 4 and tables XV and XVI for Scotland (for corrections made in the numbers, see p. 41), in tables XVII and XVIII for Narvik. Combining the data from all these regions we arrive at the following conclusions:

1. The var. *citrina* prefers *Fucus serratus* in all regions, except near Narvik, where this variety shows a preference for *Fucus spiralis*. In Brittany its absolute numbers are as large on *Fucus vesiculosus* as on *Fucus serratus*, but its frequency in relation to the total numbers of *L. obtusata* is greater on the latter alga. In Scotland this percentage is as large on *Ascophyllum* as on *F. serratus*, but its actual numbers are larger on *F. serratus*.
2. In Scotland the variety *inversicolor* and *ziczac* show a preference (absolutely and relatively) for *Fucus serratus*.
3. In Brittany the variety *fusca* is most abundant on *F. spiralis*. In Scotland both its actual number and its percentage are as high on *Fucus spiralis* as on *Fucus vesiculosus;* its percentage is as high there on *Laminaria saccharina* as on the two *Fucus* species.
4. In Brittany the variety *olivacea* shows a preference for *F. spiralis* (absolutely and relatively) and for *Ascophyllum* (relatively only), in Scotland for *F. spiralis* (abs. and rel.) and *Laminaria* (rel. only), on

Schouwen for *Ascophyllum* (both abs. and rel.), near Den Helder for *F. vesiculosus* (abs. only), and *Ascophyllum* (rel. only), near Narvik for *F. vesiculosus* (abs. and rel.) and *Ascophyllum* (abs. only).

Summarizing these facts we can say that in each locality the various varieties to some extent prefer different algae, and that for many varieties this preference may vary from one region to another; var. *citrina*, however, prefers *Fucus serratus* (low level) everywhere, whereas var. *fusca* and *olivacea* always prefer the algae of higher levels.

As to the form varieties, it appears from the tables mentioned above, that var. *pachychila* is mainly found on *Fucus serratus*, both in Scotland and on Schouwen, whereas var. *retusa* is most abundant on the algae growing higher: *Fucus spiralis* in Brittany, *Fucus spiralis* and *vesiculosus* in Scotland (on *Ascophyllum* its number is smaller there, but its percentage even slightly higher than on the two *Fucus* species), *Ascophyllum* (with regard both to numbers and percentages) near Den Helder and on Schouwen. Compare, however, what has been said about the form varieties on p. 27.

B. THE CAUSES OF THE VERTICAL DISTRIBUTION

From the foregoing it will be evident that both level and vegetation affect the distribution of *Littorina obtusata* and its varieties. We will therefore deal with them separately.

We have seen that *L. obtusata* is never found unless at certain levels and in conjunction with certain algae. This statement involves two problems, viz.:

A. Would it be possible for the species to live outside these ranges of abiotic and biotic factors, and if not, why not?

B. What innate behaviour enables the snail to remain within its zone or to reach stations where these factors are present? We will first deal with problem A, viz. with the tolerance and needs of the species with regard to ecological factors; afterwards we will consider problem B, i.e. the active responses of the species on these factors.

1. *The habitat factors and their significance*

a. *Abiotic factors (level).* 1. Submersion. EBBINGE WUBBEN kept a number of snails of the variety *olivacea* submerged in a cage provided with food (Fucaceae). After one month the snails were still alive. In nature this variety is always found at rather high levels, where it is never immersed for more than a few days on end. BROEKHUYSEN (1940) found the same for the South African *Littorina knysnaensis*, a species inhabiting the upper part of the tidal zone, where it is submerged for only a few hours at a time. This shows us that, as far as submersion is concerned, the lower limits of *L. obtusata* var. *olivacea* and *L. knysnaensis* actually found in nature are higher than their potential lower limits. This will be due to negative geotaxis, see p. 51–53 and Postscript.

The lower limit of *L. obtusata* lies at E.L.W.S., a level which falls dry but once or twice a year (see p. 38). Wilson (1935) concludes from this fact that *L. obtusata* is unable to stand permanent immersion. This is neither contradicted by the experiment of Ebbinge Wubben (which only revealed a *minimum* time of submersion tolerance for var. *olivacea*, not the *maximum* tolerance of the whole species) nor proved by the vertical distribution in nature, since the snails are able to move up and down the tidal zone of the shore (see p. 55). We are therefore not sure that the individuals found at E.L.W.S. actually stay there throughout the year. Even if Wilson were right, these movements would enable the snail to occur temporarily at still lower levels. The fact that we do not find them there cannot be explained by Wilson's hypothesis, but is most probably due to the strong negative geotaxis mentioned above.

2. Emersion. In nature emersion affects the snail through its effect on desiccation, temperature (insolation, frost), and salinity (rain!). In the laboratory, at room temperature and without direct sunlight, emersion only causes desiccation. Under laboratory conditions several species of *Littorina* have been tested with regard to the maximum time of emersion they can stand. The result may be summarized as follows:

L. muricata	> 360 days	Cooke, 1895
L. neritoides	> 210 days	Fraenkel, 1927
L. planaxis	64 days	Hewatt, 1937
L. knysnaensis	42 days	Broekhuysen, 1940
L. saxatilis	31 days	Colgan, 1910
L. littorea	23 (19) days	Colgan, 1910 (Gowanloch and Hayes, 1926)
L. obtusata	6 days	Colgan, 1910

It must be stressed, however, that these species live in different climates: *L. muricata* in a tropical climate, *L. planaxis* and *knysnaensis* in subtropical climates, *L. neritoides* in both subtropical and temperate climates, the other species in temperate and cold climates. So we must be very cautious when relating these findings to the levels at which the species live in their natural habitats. Yet, a close parallelism appears to exist (see also Postscript): their drought tolerance appears to increase parallel with the level of their habitat, with the exception of *L. knysnaensis*, which has a higher upper limit than *L. neritoides* (but its mean level of occurrence is generally lower than in the latter species). The ranges of *L. littorea* and *obtusata* are about the same, but their habitats are different and this is clearly reflected in their respective drought tolerance: *L. littorea* lives both on algae and on bare rocks, whereas *L. obtusata* is confined to algae, which protect the animals against desiccation. Probably this is the reason why *L. obtusata* is found, albeit sporadically, in places which remain uncovered for nearly a fortnight (M.H.W.S.), when, on the other hand, it can stand only 6 days of emersion (corresponding with M.H.W.) in the laboratory, without algal cover. But temporary migration to lower levels and the moistening influence of splash and spray in its natural habitat may perhaps contribute to this difference. Moreover, the upper limit is often at M.H.W.N. (see p. 38), which is *lower* than what might be expected on account of its drought tolerance.

The species of high levels must also be more tolerant to fresh water; here again a clear correlation appears to exist: the maximum periods of immersion in fresh water, which can be endured, are as follows:

L. neritoides	8 (11) days	FRAENKEL, 1927 (resp. COLGAN, 1910)
L. saxatilis	7 days	COLGAN, 1910
L. littorea	7 days	COLGAN, 1910
L. ziczac	4 days	PEARSE, 1929
L. obtusata	2 days	COLGAN, 1910

These species all inhabit temperate regions, except *L. ziczac*, which is a subtropical species.

Again we see that *L. obtusata*, although inhabiting the same level, is less resistant than *L. littorea*. This is easy to understand, since the blunt periwinkle hides under the algae both when desiccation becomes dangerous and when it starts to rain. The algae, owing to their large salt reserves, may constitute a buffer against salinity changes. *Littorina littorea*, on the other hand, also lives on bare rocks where there is no protection against fresh water. *L. saxatilis* even goes so far as to leave the fissures to feed on the rocks when it is raining.

Contrary to what has been said about desiccation and fresh water resistance, our knowledge concerning lethal temperatures hitherto does not reveal any correlation with level in the genus *Littorina*, although BROEKHUYSEN (1940) found a slight correlation for other intertidal Gastropods (including the *Littorina* species) in False bay, South Africa. *L. obtusata* has been stated to die at 42° C. (GOWANLOCH and HAYES, 1926), though living among cool sea-weeds in cold and temperate regions, whereas for instance *L. ziczac*, inhabiting bare rocks in a hot climate has been found to die at 38° (PEARSE, 1939).

As we have seen before (p. 39), the optimum level of *Littorina obtusata* ssp. *littoralis* shows a downward trend from the South to the North. This will be particularly evident from fig. 5, where these levels are indicated in a diagram.

As all observations were made in high summer, it seems highly improbable that low temperatures in the North should be the direct cause of the downward trend. Even in winter temperature will have little direct influence, since winters in Scotland and even in Narvik are rather mild and *L. obtusata* can stand —30° C for a long period (DEXTER, 1947). In my opinion the primary cause must be sought in low surface salinities, because the influence of rain is greatest at high levels and evaporation is much reduced in a cold climate. An additional explanation might be that the snail needs higher salt concentrations when the temperature is lower, a phenomenon observed in other marine animals (BROEKEMA, 1941). The fact that subspecies *typica* prefers a higher level at Narvik than ssp. *littoralis* does not contradict this: being an arctic type, ssp. *typica* must be adapted to the still lower salinities of the arctic littoral. From the point of view of ssp. *typica*, Narvik does not represent a northern climate, but the most southern conditions it will encounter.

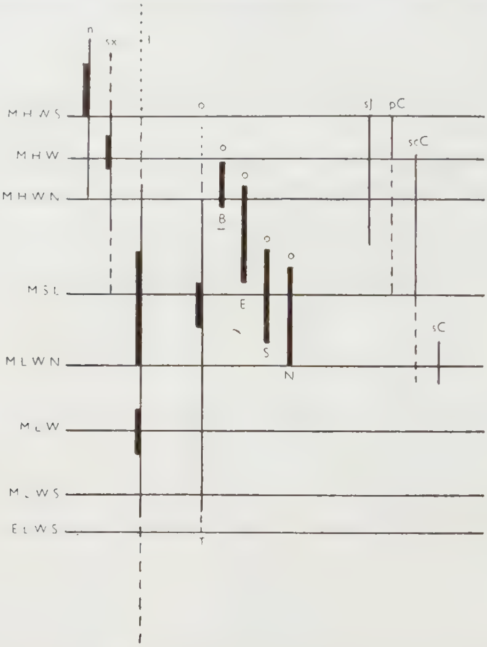

Fig. 5. Vertical range of *Littorina* species. The black lines indicate the levels of greatest abundance, the dotted lines levels at which a particular species is scarce. n = *L. neritoides*; sx = *L. saxatilis*; l = *L. littorea*; o = *L. obtusata* ssp. *littoralis*; T = total range; B = optimumlevel in S. Brittany; E = ditto in S. England; S = ditto in N. Scotland, W. Sweden and E. Canada; N = ditto in Narvik (N. Norway); sJ = *L. sitchana* in Japan (30–40° N. lat.); sC = *L. sitchana* in California (40–50°); pC = *L. planaxis* in California (32–37°); scC = *L. scutulata* in California (36–42°).

In accordance with our hypothesis that salinity may cause a downward trend of the optimum level, which becomes all the more pronounced as we go farther North, is the fact that in the rather brackish Gullmar Fjord (W. Sweden) both the upper and the lower limit of *L. obtusata* are lower than anywhere else (Gislen, 1930). It may further be stated that the same downward trend from South to North is found in the genus *Littorina* as a whole; in warmer climates it occupies higher levels, a phenomenon which, by the way, may be observed in many marine animals. In Panama a *Littorina* species has even been found to climb trees bordering the high water line and to feed on their leaves (Cooke, 1895).

Finally, an argument in favour of our theory is furnished by *L. ziczac*. This is the only species that does not fit into the scheme of parallelism between level and fresh water tolerance (see table on p. 47), since it is found at the same level as *L. saxatilis*. However, it lives in a much warmer and drier climate, where evaporation is strong and the salinity of the sea water averages no less than $36\,^0/_{00}$ (see also Postscript).

b. *Biotic factors (algae)*. As regards the influence of biotic factors, only those algae on which *Littorina obtusata* lives will be discussed here. They are of manifold importance as they offer:

1. protection against heavy surf;
2. protection against desiccation;
3. shelter against rain;
4. substratum for spawning;
5. food.

Of these needs 1 and 2 are equally well or even better met by rock fissures and tidal pools, the other ones are only fulfilled by the Fucaceae. (As regards the third point, tidal pools and fissures are probably even more unfavourable than smooth slopes, since rain water tends to accumulate there.) This explains why *L. obtusata* cannot live without Fucaceae. Point 2 has been discussed already on p. 46, point 3 on p. 47; 4 and 5 will be discussed here.

It is a well-known fact that *Littorina obtusata* spawns on the fronds of Fucaceae. At Den Helder I found eggs on all Fucaceae, particularly on *Fucus serratus*. In the laboratory (experiments 1–9, see p. 59) the animals also spawned on all Fucaceae, except *F. spiralis*. As regards feeding, the holes made in the algal fronds by feeding snails had been overlooked by me, but in the aquarium, where the number of animals in proportion to the quantity of algae was much larger, this phenomenon could easily be observed. *Fucus serratus* and *F. vesiculosus* were severely damaged here. *Ascophyllum* and *F. spiralis* were moderately attacked, the other algae were not taken for food at all. But here, just as in nature, Fucaceae were always present. The question therefore arose whether the snail is able to make use of other algae than the Fucaceae for spawning and feeding if the latter are absent.

1. Spawning. In order to investigate this problem, a large number of snails were kept in an aquarium without algae for about five days; then they were put into a bottle with circulating sea water and with a small quantity of one algal species. Special care was taken to use algae without clusters of eggs. The species used were *Ulva lactuca*, *Chondrus crispus*, *Gigartina stellata*, and—by way of control—*Fucus serratus*.

After some days (for their numbers see the figures between brackets in table XXI) many clusters of eggs had been deposited on *Fucus serratus*, none on the other algae. The eggs on *Fucus* had been laid in spite of the far advanced season (October). This seems to show that the presence of Fucaceae is indispensable if the snails are to spawn.

2. Feeding. The experiments described above also produced some information on feeding behaviour. Specimens of algae were chosen that had not been attacked before.

EBBINGE WUBBEN used *Enteromorpha* in the same way. Moreover, he kept 20 snails for six weeks in a cage in the tidal zone on the shore with *Enteromorpha* as the only alga. *Fucus serratus* as well as *Ulva lactuca* appeared to be severely attacked. *Chondrus* was attacked to a small degree. *Gigartina* and, according to EBBINGE WUBBEN, *Enteromorpha* did not suffer at all. The results show that the snail is able to feed on some of the other species if *Fucus* is absent. If present, all other algae are left untouched (experiments 1-9). In this connection it is noteworthy that, according to KUNZE (1923), algae avoided by the Isopods *Idothea granulosa* and *baltica* will be eaten after extraction. KUNZE supposed that they might contain substances poisonous to the animals. The same might perhaps be the case with *Gigartina* in our experiments, since mortality was very high on this alga.

The rate of mortality of the snails on the different algae can be seen from table XXI. The numbers between brackets denote the duration of the experiments in days.

At the end of the experiments *Fucus* and *Chondrus* were decaying, whereas *Ulva* and *Gigartina* still appeared to be in good condition. Nevertheless, mortality was highest on *Gigartina* and *Chondrus*. If we take into account the condition of the algae and the duration of each experiment, the figures seem to indicate that mortality is inversely proportional to the extent to which the algae are attacked. In all cases the variety *citrina* showed higher mortality than *olivacea*, just as in experiments 1-9. The experiments were, however, too inexact to permit further conclusions, since mortality was high in all cases.[1]

Although the algae were used separately, the preference for *Fucus serratus* was evident even now, namely from the quantitative relation between the numbers of snails found on the algae and the numbers found beside them. These numbers were in the ratio of 51:47 in the case of *F. serratus* and 8:81 in that of *Chondrus crispus*. On the other algae the distribution was similar to that on *Chondrus*.

In conclusion we may state that *Littorina obtusata* evidently needs Fucaceae for spawning and strongly prefers them to other algae as food.

2. *The behaviour of Littorina obtusata with regard to environmental factors*

a. *Responses to abiotic factors*. 1. Reaction to gravity. In the literature no mention is made of geotaxis in *L. obtusata*, although it has been studied in all other European species of the genus. All investigators, except Morse (1910) and Mitsukuri (1901), agree as to the existence of negative geotaxis in *Littorina*. Both Ebbinge Wubben and I found the same behaviour in *L. obtusata* in all our experiments.[2]

Ebbinge Wubben made a special study of the geotaxis of *L. obtusata*, var. *olivacea*. In the laboratory he placed a number of animals on a moist horizontal plate of eternite. After the snails had attached themselves to the substratum, the plate was placed in a vertical position and the movements of the animals were observed. None of them moved downwards; they either climbed the plate or moved sideways for a short distance. The results are summarized in table xxii. These readily show that in all cases the majority of the individuals displayed negative geotaxis. Since this was also the case in a completely dark environment without water, but with a saturated atmosphere throughout, it will be evident that the upward movement is not caused by phototaxis or by a tendency either to escape from the water or to reach drier air.[3]

The upward movement, if it takes place in water, is not due to the need of water with a larger oxygen supply, since it is also observed in aquaria with (vigorously) circulating sea water. Kanda (1916) showed that *Littorina littorea* moves upward even when the oxygen concentration decreases in that direction. Fraenkel (1927), working with *L. neritoides*, proved that gravity is responsible for the upward movement,

[1] In the experiment made by Ebbinge Wubben mortality was low in spite of the fact that *Enteromorpha* was not eaten: after 6 weeks 3 animals out of 20 had died.

[2] All observations were made in summer. It is not impossible that in winter geotaxis is weaker or even positive.

[3] A comparison of the left and right halves of the table shows that the conditions of exposure and immersion during the experiment do not influence geotaxis even to the slightest extent.

because animals placed on a high speed rotation disk moved towards the axis. KANDA (1916) assumed that gravity compels the animals to take up a position in which the heavy shell is hanging down, in which position they cannot but move upwards. FRAENKEL showed this opinion to be erroneous: if the snails are submerged and the shells made lighter than the surrounding water by attaching pieces of wax to them, the upward movements are continued. Probably gravity acts upon the statocysts which are highly developed in the genus *Littorina*.

EBBINGE WUBBEN also studied the influence of periods of previous immersion and emersion on the negative geotaxis. For this purpose he kept the animals submerged (resp. exposed to the air) for periods of different lengths and then tested them with regard to their geotaxis. The results (see table XXII B) show that geotaxis remains constant even after long immersion. The same was observed in *L. littorea* by HAYES (1927, 1929). EBBINGE WUBBEN likewise denies the influence of emersion (table XXII A), but in my opinion a slight influence was possibly shown by animals tested in a dry aquarium, although it must be admitted that the lower percentage of animals showing negative geotaxis after exposure to the air for 60 hours, viz. 68 % only, is based on too small a total number of animals investigated (19 specimens) to be reliable. It must be remarked that EBBINGE WUBBEN only observed whether the snails were negatively geotactic or showed no geotaxis at all. The distance covered in climbing by the active animals was not measured. According to GOWANLOCH and HAYES (1926) the negative geotaxis of *L. littorea* steadily decreases to zero during desiccation, even if followed by immersion, provided this immersion does not last sufficiently long to let the snails recover. According to KANDA, who worked with the same species, negative geotaxis may even become positive after desiccation.

EBBINGE WUBBEN also investigated whether there are differences in geotaxis between individuals found at different levels on the shore. To this end he collected animals at a high level and at a low level; the animals of each group were marked and laid down on the shore, partly at their original level, partly at the level of the other group. As he thought it possible that those collected at a low level had recently migrated there, he also used animals collected at a high (!) level after he had kept them (in a cage) at a low level for a month (group D). The result (table XXIII) was that no difference was to be found between animals of different levels. All of them tried to reach the highest level of the algal belt. The snails used by EBBINGE WUBBEN all belonged to the variety *olivacea*. On p. 61 we shall see that animals of one variety, collected on different algae (which generally implies: at different levels), do not show any difference, due to level, as to their preference for certain algae. The individuals of one variety may therefore be assumed to prefer the same level.

This is contrary to the view of Gowanloch and Hayes (1926) and Hayes (1927), who believe that animals of high levels show a stronger negative geotaxis than those of low levels, which, according to them, makes the snails return each to its own particular level after displacement. From their papers it appears that the experiments concerning this point were made with *L. littorea*. They were carried out with far too small a number of animals and the results appear rather doubtful.

I myself compared the behaviour of different varieties, viz. *citrina* and *olivacea*. A number of snails were laid in complete darkness on a concrete table with vertical wooden walls. The snails were immersed in running sea water reaching 8 cm high. Most of the animals immediately started to climb the walls and they continued doing so after they had left the water. The variety *citrina*, though of smaller size, proved to climb faster than the variety *olivacea*, thus reaching higher levels in the beginning. After one hour it was overtaken by the variety *olivacea* and still later on the positions had been reversed. Many *citrina*'s must therefore either have crawled back into the water or dropped down. The distribution of the animals was then as given in table XXIV.

Thus, in the end, the distribution had become similar to that in nature. The same happened in experiments 1–7. Here the proportion between the numbers of animals above and below water was 2.17 in the variety *olivacea*, 1.74 in the variety *citrina* (based on 2000 animals). Consequently, we see negative geotaxis is stronger in var. *olivacea* than in var. *citrina*.

2. Reaction to light. The influence of light has been studied in several *Littorina* species by a number of workers, but not in *Littorina obtusata*. All authors, except Haseman, agree that *Littorina* shows so-called negative phototaxis, which means that in most experiments and in nature the species examined move away from the higher light intensities to which they are exposed.

I myself did not make any special observations on the influence of light; yet some of my experiments produced some information in this respect. In experiments 1–7 the tiles exposed to the light always proved to contain smaller numbers of animals than those lying in the shade, irrespective of the species of algae present on the tiles. By adding the numbers of animals of each category from all experiments, we eliminate the specific influence of the algae, so that the remaining differences may be exclusively attributed to the influence of light. The quantitative relation between the numbers of animals on the shaded tiles and those on the tiles exposed to light is then found to be 1.70:1 in the variety *olivacea* and 1.48:1 in the variety *citrina*. This means that there is a clearly noticeable preference for weak light, which is different in both varieties. As these figures are based on nearly 2000 animals, this result is quite reliable from a statistical point of view, the more so as the same difference was found in each of the separate experiments, but not in experiment 8, which was carried out in complete darkness. So it will be evident that the variety *olivacea* has a stronger dislike of light than the variety *citrina*. At first sight this may seem rather surprising, since the former variety inhabits higher levels on the shore and is consequently exposed to a larger total amount of light. But it will become quite understandable as soon as we realize that the variety *olivacea* is mostly found *among* the algae, and is covered by them, whereas the variety *citrina* mainly lives *on the surface* of the algal cover.

In nature "phototaxis" and geotaxis will normally counteract each other. The same may be said to be the case in Ebbinge Wubben's experiment summarized in table xxii, in which a daylight lamp was hung over the aquarium in some of the tests. The table shows that in this case geotaxis was slightly counteracted, but by no means neutralized by phototaxis (see also Postscript).

3. Reaction to vertical water movements. Vertical water movements greatly influence the behaviour of *Littorina obtusata*. This influence is complicated and both of a direct and indirect nature. It consists in:

1. *Desiccation effect.* When exposed to the air at low tide, the animals keep crawling about as long as the substratum or the snails themselves remain in a moist condition. Ebbinge Wubben, studying the movements of the snails on a stretch of shore from which the algae had been removed, observed that they ceased crawling and retreated within their shells as soon as the stones had dried up. As a result of this, both gravity and light lost their effect at that moment.
2. *Light effect.* Since light intensities are much higher above water then below, "phototaxis" will become much more effective as soon as the animals leave the water or are no longer covered by it at ebb tide.
3. *The effect of draining water.* In the experiment mentioned sub 1 Ebbinge Wubben noticed that, when the falling tide passed the animals on the shore, they started moving sideways and downwards. It looks as if negative geotaxis becomes positive when a thin layer of water is draining away over the animals. This was also observed by Mitsukuri *(Littorina exigua)* and Haseman (mainly *L. littorea*), but the existence of this phenomenon was denied by Kanda.

The effect produced must be caused by the water surface, for, when completely submerged, *L. obtusata* is not affected by water currents.[1] The reaction caused by draining water is not to be considered as a simple inversion of the natural geotaxis, but as an independent effect which counteracts the negative geotaxis. This is shown by the following experiment. I placed animals at the base of a vertical glass plate, along which sea water was constantly running down. The snails moved upwards, most of them only for a short way, and stayed there for days on end. So, here, their geotaxis was only *neutralized* by their reaction to draining water. The explanation might be that geotaxis was rather strong here: KANDA has shown that geotaxis in *Littorina littorea* is stronger (or rather: more effective) on a smooth surface than on a rough one and increases when the slope becomes steeper. In the field observation made by EBBINGE WUBBEN the surface was rough and the slope rather gentle. Hence, geotaxis was probably weak there and therefore outbalanced by the reaction to draining water.

4. Tidal rhythm. From what has been said above, it may be expected that the animals are driven upwards by negative geotaxis at rising tide, hampered by surface tension and negative phototaxis when leaving the water, prevented by desiccation from climbing far ahead of the rising water level and compelled by the effect of draining waves to return at falling tide. A rhythmical migration up and down the slope of the shore, synchronous with the tides, would be the result.

Several authors (MITSUKURI, BOHN, MORSE, and HASEMAN) believe they have observed such migrations in *Littorina*. *L. neritoides* would not exhibit such movements in the Mediterranean, owing to the lack of tides. BOHN even stated (but he is contradicted on this point by MORSE, and by HASEMAN) that the snails kept crawling up and down in an aquarium with constant water level for some time after they had been captured in nature; according to him the movements even coincided with the tides outside and covered a larger range at the time of spring tides!

EBBINGE WUBBEN studied the phenomenon on a part of the shore, from which all algal vegetation had been removed. He found that the animals left the water and climbed the shore till desiccation stopped them. As soon as the first drops of sea water of the rising tide moistened them, they attached themselves to the stones with their feet and, after being immersed, started climbing, but stopped already before the sea had reached the high water mark (except a few animals that climbed as far as E.H.W.S.!).

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[1] An other effect of surface tension is the hesitation shown by *Littorina*'s, which have to pass a water surface, both when entering and when leaving the water. See also Postscript.

A new activation took place when the falling tide passed the animals, stimulating them to move sideways and downwards, though this movement was much slower than the upward one. Consequently, they finally reached a level where the stones had dried up already; here they waited for the rising tide, which drove them upwards again.

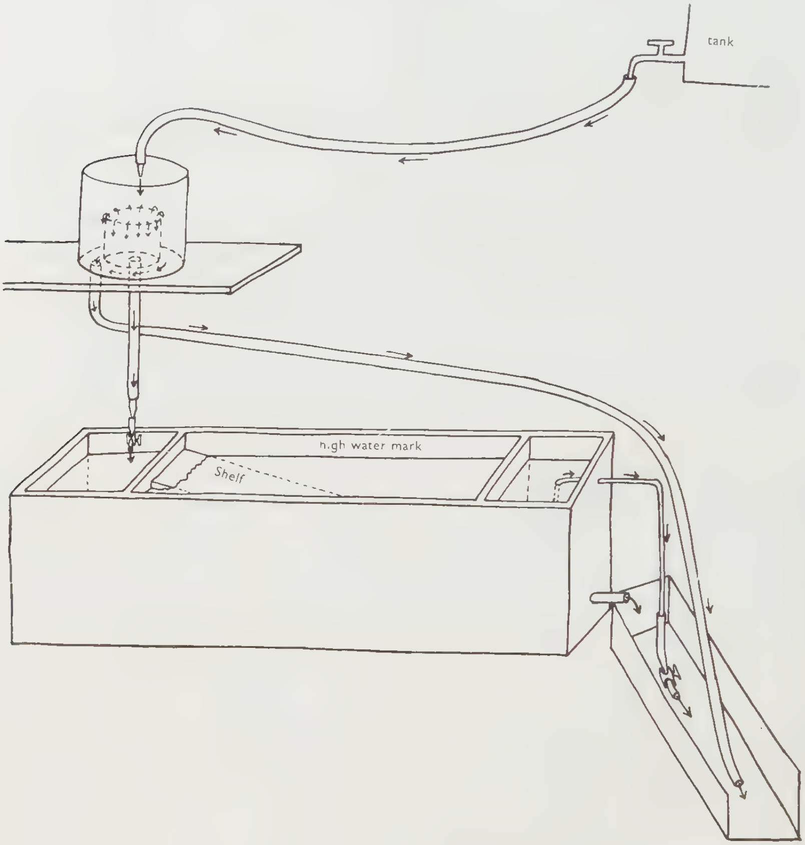

Fig. 6. Tidal aquarium.

Tidal migrations up and down the slope of the shore therefore seem to occur also in *L. obtusata*, at least where there are no algae, but the range of their movements appears to be smaller than the tidal amplitude.

In order to investigate this problem, I constructed an aquarium with running sea water and artificial tides; a mechanical device made the water level rise and fall in accordance with the cycle of natural tides and with an amplitude of 33 cm. In the aquarium a wooden shelf of 220 by 30 cm, covered with stone tiles (the same as used in exp. 1–7), and divided into sections of 10 cm, was placed in a very oblique position (see figs 6 and 7). The greater part of the shelf was exposed to the tides, only small parts were permanently dry or immersed. A number of animals were evenly distributed over its full length; 453 animals of var. *citrina* and 340 of var. *olivacea* were used.

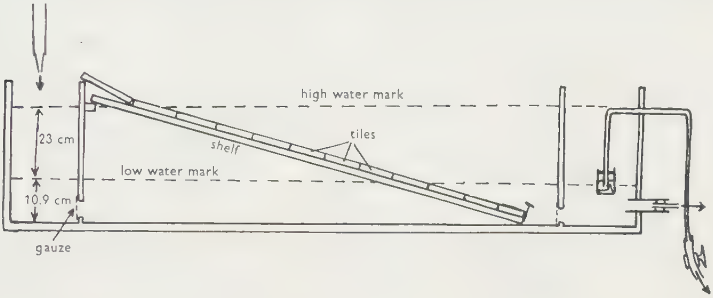

Fig. 7. Longitudinal section through the tidal aquarium.

No rhythmical movements were observed. Most animals left the shelf and climbed the vertical walls. After a short time most of them had concentrated just above high water mark, both on the walls and on the shelf. Their distribution did not undergo any further change; a graphic representation of it is given in fig. 8. This figure shows the following facts:

1. The majority had concentrated in a belt from 0 to 6 cm above high water mark. The second maximum (below 26 cm depth) has no real significance, as it includes the whole bottom of the aquarium; the very large surface probably accounts for the large total number at this depth.
2. The two varieties show an identical distribution pattern.

The difference in the results obtained by Ebbinge Wubben and myself is probably due to the different experimental conditions. A gentle slope with a rough surface, direct sunlight, desiccation caused by sun and wind, and repeated draining caused by the waves, must have combined in the field experiment to hamper upward migration and induce a return to lower levels.

In the aquarium negative geotaxis must have been strong on the vertical walls, "phototaxis" must have been weak, since only diffuse daylight penetrated into the room. Moreover, desiccation was reduced by a moist atmosphere and lack of wind. The concentration just above high water mark may easily be explained as the result of negative geotaxis combined with reduced desiccation. The latter only stopped the animals a few centimeters above high water mark, where they were out of reach of the water. Since there were no waves, there was no draining to make them return.

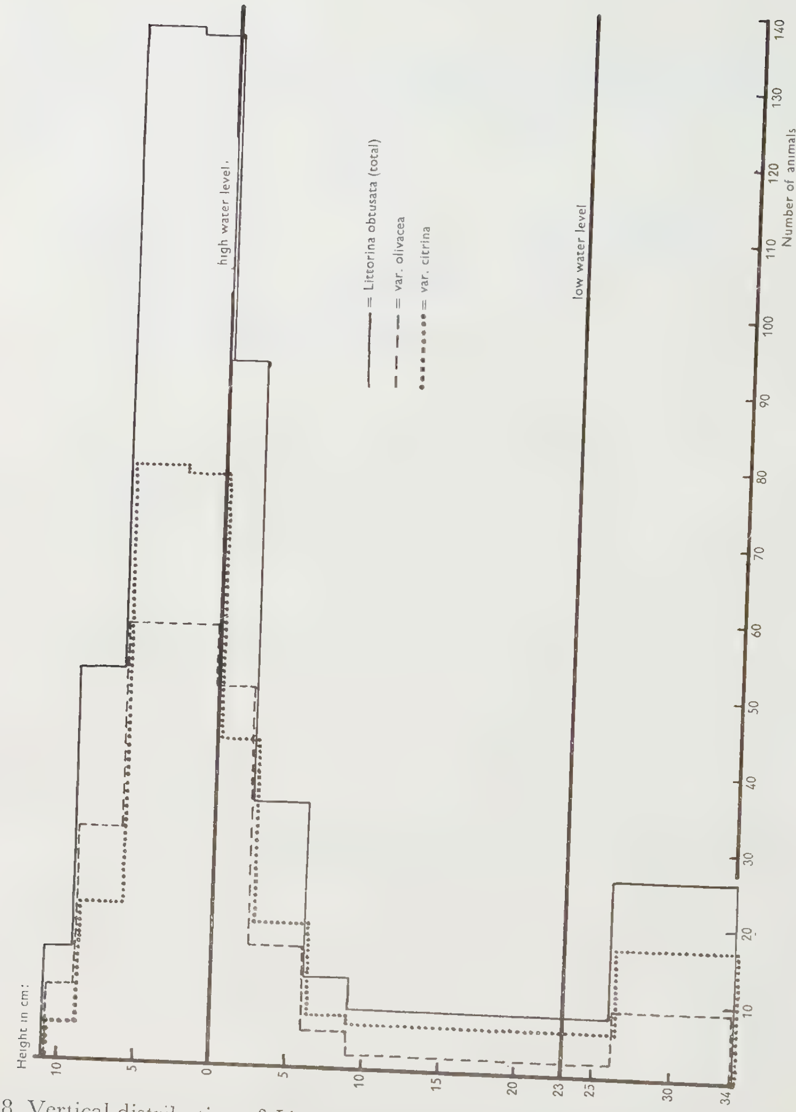

Fig. 8. Vertical distribution of *Littorina obtusata* in the tidal aquarium without algae (14 X 1948).

b. *Response to biotic factors.* 1. The preference for certain algae. We found that in nature *Littorina obtusata* is much more abundant on Fucaceae than on other algae (chapter IIIA 2) and that it needs them as food and as a substratum for spawning (chapter IIIB 1b). We also found, however, that the occurrence of the snails is influenced by abiotic factors. The influence of level should therefore not be neglected. This is clearly demonstrated in the Gullmar Fjord (W. Sweden). Contrary to what is the case in other regions, *L. obtusata* is rare on *Ascophyllum* here and not found at all on *Fucus serratus*. Now, in this locality these very algae happen to grow at abnormally low levels: *Ascophyllum* grows around E.L.W.S. (at 20–60 cm below M.S.L.), *Fucus serratus* grows below E.L.W.S. (at more than 50 cm below M.S.L.). Since *L. obtusata* is never found below E.L.W.S. (which, here, lies 40 cm below M.S.L.) the abiotic emersion complex probably accounts for the abnormal state of affairs in the Gullmar Fjord.

Another indication of the influence of level is given by the difference in vertical distribution between the varieties *citrina* and *olivacea*. Both are abundant on *Fucus vesiculosus*, but the former mainly inhabits the lower half of the zone formed by this alga, the latter variety occupies its upper half.

The first question to be considered therefore is: what species of algae are frequented and which of these are preferred by the blunt periwinkle if the influence of level is eliminated? In order to investigate this problem the following aquarium experiments were carried out. It should be realized that, besides the influence of level, wave action was eliminated at the same time.

Comparable quantities of *Ascophyllum nodosum*, *Fucus vesiculosus*, *F. spiralis*, *F. serratus*, *Ulva lactuca*, *Chondrus crispus*, *Gigartina stellata*, and *Porphyra laciniata* were brought together in an aquarium, in such a way that equal parts of each species were immersed and uncovered. All algae had been carefully cleared of *Littorina*'s before.

The aquarium was a wooden gutter, 200 cm long, 45 cm wide and 25 cm high, filled with sea water up to 8 cm above the bottom. A constant slow flow of water was maintained, and the snails were prevented from escaping by gauze at the inflow and outflow. The gutter was covered with glass plates.

The algae were laid down on 8 out of 10 obliquely placed tiles,

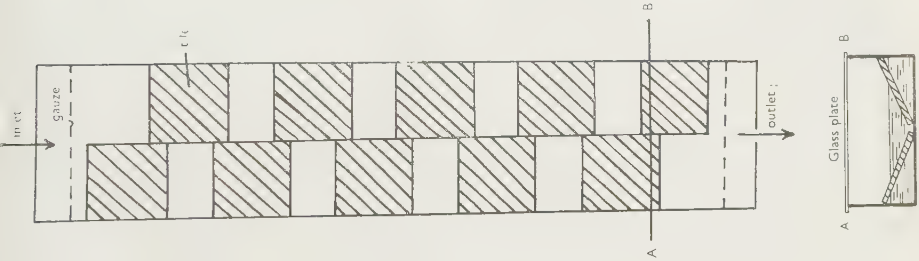

Fig. 9. Arrangement of the tiles with algae in the aquarium (experiments 1–7).

arranged in two alternating rows (fig. 9). In each row one tile was kept bare. These two tiles, placed far apart, served as controls.

Experiments were carried out with snails of the variety *citrina*, collected on *Fucus serratus* and on *F. vesiculosus* separately, and with individuals of the variety *olivacea* from *F. vesiculosus* and *Ascophyllum nodosum*. *F. vesiculosus* was the only kelp on which both varieties could be collected in sufficient quantities. The snails were laid down on the bottom of the aquarium in the open spaces between the tiles, evenly distributed all over the gutter. The numbers of animals used are summarized in table XXV.

Four to five days proved sufficient for the animals to make their choice. After 6 days the algae (especially their immersed parts) began to decay, causing the periwinkles to die (experiments 5 and 7: mortality 50–75%!). The animals did not leave the decaying algae, but died on them. Their distribution therefore remained the same, and the results of experiments 5 and 7 may be considered to have the same value as they would have had if the experiments had sooner stopped. Mortality was low (5–18%) when the experiments lasted a shorter time.

The sequence in which the different species of algae were placed on the tiles was the same in experiment 1 and 2, except that the left and the right row were interchanged and the sequence within each row reversed. In the same way the arrangement in exp. 4 is the reverse of that in exp. 5. The arrangement of exp. 6 is identical with that of exp. 4, the arrangement of exp. 7 is identical with that of exp. 5. Left and right were interchanged in order to eliminate any possible influence of light (one row was more shaded than the other); the sequence in each row was reversed in order to eliminate any possible influence of the direction of the water current.

The positions in which the algae were placed in relation to one another were the same in experiments 1–3, each alga being surrounded by the same other algae in all cases. Their relative positions were different in experiments 4–7, (in none of these the algae were arranged in the same way as in exp. 1–3) in order to eliminate any possible influence of competition between the algae in attracting the snails. This proved to have indeed a strong influence on the distribution of the snails.

The results are given in tables XXVI and XXVII. Out of a total number of 2823 snails used 2314 were found back after the experiments. Of this number about 58% were found on algae, the percentage being the same for var. *olivacea* and *citrina*. If we add the numbers of the two varieties, the following figures are obtained:

Fucus spiralis	306	1076
F. serratus	289	
F. vesiculosus	250	
Ascophyllum nodosum	231	

Ulva lactuca	81	253
Chondrus crispus	77	
Porphyra laciniata	57	
Gigartina stellata	38	

There is clearly a preference for the Fucaceae as compared with the other algae under consideration. It is remarkable, though, that 3.5%, 2.5%, and 1.7% were found back on *Ulva*, *Porphyra*, and *Gigartina* respectively, on none of which the snail was observed in the field.

On the whole, animals of one variety, collected on different algae, showed a similar behaviour, but some remarkable facts came to light. It looks as if the variety *olivacea* collected on *F. vesiculosus* had a greater relative preference for *Ascophyllum* than for *F. vesiculosus*, and vice versa. The variety *citrina* from *F. serratus* had a stronger preference for (both *serratus* and) *vesiculosus* than the same variety collected on *F. vesiculosus*. Both varieties seem to have a stronger dislike to *Porphyra* in case they are collected on *F. vesiculosus* than when collected on *F. serratus* or *Ascophyllum*. We might ask whether there may be a shifting in the preference for a particular food after a certain alga has been consumed for some time.

Most interesting are the differences between the two varieties.

The preference for Fucaceae is more pronounced in var. *olivacea* (ratio Fucac.: non Fucac. = 613:91) than in var. *citrina* (ratio 463:162) and var. *olivacea* is found in far smaller numbers on *Chondrus crispus* than var. *citrina* (in the field only var. *citrina* is found on *Chondrus*).

Within the group of Fucaceae the variety *citrina* clearly has a preference for *F. serratus*, although it is also abundant on *F. spiralis*, on which it is rarely found in nature. As regards var. *olivacea*, the results are rather doubtful: its preference shifts from one alga to an other in the various experiments.

Identical arrangements of algae in experiments 4 and 6, and likewise in exp. 5 and 7, produced identical results as to which alga species is liked best. Illumination, position of the algae relative to the inflow and outflow and to the positions of other algae, were all found to influence the results. I therefore tried to make corrections for these sources of error separately and in combination with each other; the results are given in table XXVIII. It shows that the preference of var. *citrina* for *F. serratus* remains most pronounced in all cases, but that the *average* preference of var. *olivacea* has shifted from *F. spiralis* to *Ascophyllum nodosum*. The separate experiments, however, are still found to produce different results for this variety.

We must therefore assume that the lines on which the experiments were conducted have given rise to unknown errors. I tried to eliminate these errors by a different arrangement (exp. 9). The green and red algae were omitted, while the 4 Fucaceae were placed in a circle with the animals in the centre. Since absence of light had proved not to influence the ability of the animals to choose the right algae (exp. 8, table XXXIII, the experiment was carried out in complete darkness. The effect of currents was eliminated by the use of a wet table without flowing water.

The result (table XXIX) is rather surprising, as both varieties now show a preference for *F. serratus*. As regards var. *olivacea*, this result neither agrees with the overall results of exp. 1–7 nor with the distribution of the animals found on the algae *above water* in these experiments (cf. table XXX). Unfortunately, there was no time left to repeat exp. 9 with larger numbers of animals.

In conclusion, we may state that the preference of *L. obtusata* for Fucaceae, so evident in nature, is maintained when all algae are offered at the same level and with the elimination of wave action; probably the snails are attracted by the Fucaceae; the preference for the latter is, however, less pronounced in the aquarium, probably because the level of the algae also influences the preference of the snail. This is also proved by the fact that in these experiments var. *olivacea* is much more abundant on *Fucus spiralis* (which grows high!) and *Fucus serratus* (which grows low!) than it is in nature, and by the fact that in the aquaria var. *citrina* is much more abundant on *Fucus spiralis* and *Ascophyllum* than in nature, where these two algae occupy zones above the optimum level of this variety.

In nature *Littorina obtusata* is not found on some algae which grow at the same level as the Fucaceae, for instance *Himanthalia lorea*, *Chondrus crispus*, and *Gigartina stellata*. In the above experiments, however, some animals were found on *Chondrus* and *Gigartina*. This may indicate, since the absence of differences in level cannot have played a role here, that the diminution of wave action may have been of influence. Should this assumption be right, the distribution of the snail in relation to the different algae in nature would be caused by: 1. attraction by the Fucaceae, 2. the influence of level, 3. wave action.

2. The perception of the algae. Judging from what is known about marine animals generally, it seemed likely that the snails would find the right algae from some distance by scenting them. For this reason some experiments were initiated by VERWEY after my own investigations had been brought to an end. These experiments, which were of a preliminary nature, are described here in a very concise form because in 1953 VAN DONGEN enlarged their scope. VAN DONGEN's results will be published as a separate paper in this journal.

VERWEY's experiments were carried out in a shallow concrete aquarium of 200 by 90 cm, with walls of about 20 cm high. Sea water was kept flowing over its bottom from one end to the other. At the downstream end a number of snails were placed, and pieces cut from the fronds of *Fucus serratus*, *F. vesiculosus*, or *Ascophyllum nodosum* were placed around the water inflow. The distance between the snails and the algae was about 150 cm. By way of control the experiments were alternately carried out without algae. Each experiment took 12–24 hours. After that period the numbers of snails present around the water inflow were counted. The best results were obtained in quite shallow water, less than 1 cm high; in somewhat deeper water the snails left the water and crept on to the walls as soon as possible. The experiments were partly carried out in daylight, partly during the night. In between the experiments the snails were regularly given algae at the end from which they started. After each experiment the bottom of the aquarium was thoroughly cleaned to make sure that there would be no traces of algal scent in the controls. Only the experiment of 22 X took place without preliminary cleaning; its numbers have therefore been omitted from the calculations. The results are given in table XXXI.

It follows from this table that when there are no algae near the water inflow, only 3,5 % of the snails collect near the inflow, as against about 22 % when algae are used. This means that the algae attract part of the snails over a distance of 150 cm. In one or two experiments the attraction was caused by only a few pieces of *Fucus* of about 1 decimetre length.

My own experiments with regard to scent perception in *Littorina obtusata* produced no positive results. Here, too, water first flowed through the algae and then reached the snails. Instead of one alga several species were used at the same time (nl. *Fucus serratus*, *Ascophyllum nodosum*, *Chondrus crispus*, *Gigartina stellata*, and *Ulva lactuca*). They were separated from each other by vertical partitions parallel to the stream. The snails were prevented from reaching the algae by a gauze. The experiments were carried out in complete darkness. The negative result may have been caused by the fact that the water was too deep and the side walls too near the snails: out of 283 animals used 219 had climbed the walls and only 64 were found on the gauze facing the algae. Their distribution did not show any preference for certain algae, which may have been due to the small number.

The fact that the snails are able to scent the algae does not exclude the possibility that other senses play an additional role in orientation. Therefore, taste and vision were also studied.

In order to isolate those properties of algae which affect taste extracts were prepared from the different species. The algae were cut fine in a mincing-machine and then ground down in a mortar after the addition of carborundum powder or, later on, chemically refined sea sand. The pulp was strained through a cloth, the liquid thus obtained was filtered and solidified by adding a solution of agar or very pure gelatine in sea water. This substance was left to set into thin rectangular plates, each containing the extract from one alga species. The same algae were used as in experiments 1–7. There were two control plates without an algal extract. The plates were laid down on the bottom of an empty glass aquarium. They were separated from each other by narrow wooden laths reaching up to the surface of the plates. Thus any possible exchange of substances among the plates through diffusion was prevented, yet a free circulation of the animals was guaranteed. These were evenly distributed over the plates and kept moist by sea water being sprinkled over them. The resulting distribution (see table xxxii) clearly shows that the snails do not prefer the extracts from the fucaceous algae. The same negative result was obtained in an experiment in which the extracellular slimes of different algae had been smeared on a moist glass plate by rubbing the algae over them; Ebbinge Wubben made a similar experiment, with an equally negative result.

We must conclude from these results either that taste stimuli are not involved in the perception mechanism of the snail or that the method adopted was unsuitable to bring out the part played by taste in the discrimination between the algae.

Vision was studied both by the elimination of light and by the elimination of all but the visual properties of the algae.

In the first experiment the algae were arranged in the same way as in experiments 1–7 (see p. 59), but *Fucus spiralis* was left out. The snails had to choose between the different species of algae in complete darkness. The results are given in table xxxiii.

From this table it is evident that the snails are able to choose the right algae in darkness as well as in daylight.

In the second experiment 6 vertical partitions were arranged radially on the bottom of an empty aquarium; they were covered with a glass plate, which was moistened with sea water, and were closed at the outer end. One of the sectors was left empty, the other five were completely filled with one alga species each. I used for this purpose *Chondrus*, *Ascophyllum*, *Ulva*, *Gigartina*, and *Fucus serratus* in the sequence given here. The idea was that the snails would not be able to scent the algae, and that a certain choice would therefore be due to optical stimuli.

It should be added that some of the sectors were slightly more illuminated than others.

50 Animals of the variety *citrina* and 50 of the variety *olivacea* were put down in the centre of the plate. After two days the distribution of the animals underwent no further significant change. It is reproduced in table xxxiv.

The experiment shows that, if scent is eliminated, the place of the snails on the algae is determined by the degree of illumination of the sectors and not by the colour of the algae.

The experiments mentioned both point to the same conclusion: that the snail probably does not find its algae by optical means.

No experimental arrangement could be devised, which would eliminate all properties of the algae except the tactile ones. Consequently, the question will remain unsolved whether tactile stimuli may play an additional role in the mechanism by which the snails perceive the algae. If such stimuli exist at all, they will have to be sought in the microscopical, not in the macroscopical structure of the algae, since the snail prefers algae both with a rough and with a smooth surface *(Fucus serratus*, *F. spiralis*, *Laminaria saccharina*, and *Pelvetia* resp. *Ascophyllum nodosum)*, and also avoids algae of both categories *(Gigartina* resp. *Himanthalia*, *Laminaria digitata*, *Ulva*, *Porphyra*, and *Alaria)*. The possibility of plain tactile stimuli offered by the internal structure of the algae may be rejected as well, since the blunt periwinkle feeds on tough Fucaceae and, when these are not to be found, on the very soft *Ulva lactuca;* on the other hand, it does not feed on *Himanthalia* or *Gigartina*, which are at least as tough as *Ascophyllum.*

Summarizing, we may say that *L. obtusata* finds the proper algae especially by means of their scent (chemotaxis). Other stimuli from the algae probably play no role.

3. *Synthesis: The combined effect of algae and abiotic factors on the vertical distribution*

Since it has been demonstrated that both algae and abiotic factors affect the vertical distribution of the snail, we will finally have to consider their combined influence.

a. *The species as a whole.* On p. 38 we found that the upper limit of the species often lies at M.H.W.N. or even lower, depending on the upper limit of the algae. On p. 47 we saw that its drought tolerance would enable the snail to reach a higher level, viz. up to M.H.W. Indeed, Ebbinge Wubben found that, if the algae are removed from the shore, the snails may reach a higher level than their normal upper limit (which at Den Helder is M.H.W.N.), viz. about half way between M.H.W.S. and M.E.H.W.S. (see p. 55 and table XXXV). In his experiment the snails disappeared again from this level after three days, but were still up to about 30 cm above M.H.W.N. then, i.e. to the very limit of the zone which is awash or at least receives spray twice a day. Consequently, we may assume that the presence of algae is the decisive factor determining the upper limit in nature. In this connection an other experiment made by Ebbinge Wubben is of much interest. He removed the upper algal belt from part of the shore and placed 100 specimens of *L. obtusata* on the algae just below the bare zone. After 10 days only 3 of them had left the algae and even those were found on small fragments of algal fronds that had escaped removal. He further found the attraction of algae to be so strong that even at high tide, when both algae and snails were well under water, no animals were found above the algae. Ebbinge Wubben also attached algae above their upper limit on the shore to see whether they would allow *obtusata* to live above M.H.W.S. His experiment did not meet with success, however, since the algae soon died.

Negative geotaxis, resulting in upward movements of the snail, also occurs when algae are present, but its effectiveness depends on the breadth of the algal belt. Ebbinge Wubben laid out a number of snails on a part of the shore covered by a broad zone of algae. They showed a clear tendency to move upwards as long as there were algae. He laid another number of snails on a stretch of the shore with very few algae. These animals were partly laid on stones, partly on a tuft of algae, both at a low level. The algae proved to prevent any upward migration (see table xxxvi). Ebbinge Wubben found that the snails only leave tufts of algae if other tufts are to be found higher up the shore. He assumes that the algae will be abandoned only if the animal observes other algae, so that its negative geotaxis is not counteracted by the inclination not to leave algae. We now know that the snail scents the algae at some distance, so that Ebbinge Wubben's assumption may be right.

As we have seen (p. 56) *L. obtusata* may move up and down the slope of the shore with the tides, when there are no algae. The question may now be asked, whether this is also the case under normal conditions. No observations were made concerning this question, but from the foregoing it will be evident that in the case of a very narrow algal zone such migrations will hardly be possible. In case of a broad zone of algae they might occur, but even then they must be of minor importance, as they do not cover the whole tidal range and are not performed by all animals simultaneously. This is evident from the fact that several varieties prefer only one or two Fucaceae each and, therefore, will not move up and down the whole tidal belt. For instance, the varieties of the higher zones (e.g. var. *olivacea*) are not found at the lower levels, even at low tide.

The influence of the attraction of the algae is also demonstrated by experiments 1–7 so far as var. *olivacea* is concerned. In the wooden gutter the proportion between the animals of this variety found above water and those found below proved to be higher in the absence than in the presence of algae, the proportions being 8.9 and 2.2 respectively.

Yet, it seems inconceivable that in experiments 1–7 animals were found above the algae at all since in nature they keep to the highest algae. Ebbinge Wubben, who found the same phenomenon in similar experiments, ascribed this abnormal behaviour of the snails to the absence of tides in the aquarium; he assumed that the animals must be stimulated to search for the algae through alternating immersion and desiccation. I consider this improbable, since in my experiments 1–7 the animals did find the right algae without alternating immersion and desiccation. I therefore suppose that for part of the animals negative geotaxis was stronger in these experiments than in nature owing to the presence of vertical aquarium walls nearby, the weak light in the experimental room and the strongly reduced evaporation. On the shore the geotaxis is probably outweighed by the combined action of chemotaxis, negative phototaxis, desiccation and the effect of draining water.

The upper limit of the species as a whole thus appears to be determined by that of the Fucaceae only. The lower limit is often determined by that of the Fucaceae as well, but when the latter reach well into the sublittoral belt the lower limit is probably caused by the combined action of geotaxis and phototaxis. Finally, surf may sometimes modify the lower limit (see p. 33). The level of greatest abundance seems to be determined by the level of the favourite algae, the thickness of the algal cover and the effect of the tidal regime upon the relative influence of gravity, light, desiccation and the effect of draining water.

b. *The varieties.* The vertical distribution of the varieties cannot be explained on the basis of their preference for different algae alone. The influence of immersion and emersion is evident. For instance at Den Helder both the varieties *citrina* and *olivacea* are abundant on *Fucus vesiculosus*, but the former dominates in the lower half of the belt formed by this sea-weed, the latter variety in the upper half. The variety *olivacea* is rarely found on *Fucus serratus*, except on those specimens which happen to grow exceptionally high, among *Fucus vesiculosus* or *Ascophyllum*. Finally, this variety is particularly abundant on *Fucus spiralis* in places where, owing to the absence of *Ascophyllum*, it grows at lower levels than is normal.

While the upper limit of var. *olivacea* coincides with that of the species as a whole and is consequently determined by the algae alone, the lower limit of var. *olivacea* and the upper limit of var. *citrina* are determined by the immersion-exposure-complex as well, the differences in range between the two varieties being probably partly due to the different degrees of negative geotaxis (see p. 53).

IV. SUMMARY AND GENERAL CONCLUSIONS

Littorina obtusata (L.) is a temperate-boreal marine Gastropod, found on both sides of the North Atlantic. It is restricted to the intertidal belts of rather sheltered, rocky coasts with clear, salt water, where it lives almost exclusively on the fronds of the large brown algae *Fucus* and *Ascophyllum*.

The distribution, relative abundance and vertical range (particularly in relation to algal zonation) of the species, its subspecies and varieties were studied by the author in the following regions: S. Brittany, Holland, N.W. Scotland and N. Norway. At the Zoological Station at Den Helder an experimental research programme was carried out in order to analyse the causes of the vertical range. The author, working with var. *citrina* and *olivacea*, mainly analysed their relations to the algae; EBBINGE WUBBEN, working with var. *olivacea*, analysed the relations to abiotic factors and the combined influence of these factors and the algae.

In the first chapter the horizontal distribution and its causes are discussed. *L. obtusata* comprises two subspecies, gradually merging into each other, viz. the arctic subsp. *typica* (S. limit near Narvik) and the temperate subsp. *littoralis*. This paper chiefly deals with the latter, which can be subdivided along two independent lines into a number of colour varieties and a number of form varieties. It is argued that most of the former are genetically distinct (except var. *reticulata*, which is probably a juvenile stage of var. *fusca*), whereas the so-called form varieties perhaps represent nothing but phenotypical variations.

As regards the geographical distribution, it is remarkable that some varieties are more abundant in the North, others in the South (cf. tables I and II). It is pointed out that the area over which the species is distributed is primarily determined by historical and geographical factors, in the second place by temperature (that of the surface layer must not exceed 20° C in summer), in the third place by salinity (species absent from the Baltic Sea and many estuaries, owing to too low salinities, below about $15\text{-}10\,^{0}/_{00}$). Local distribution is further limited by the need of Fucaceae, of sheltered rocky coasts and of clear water. Heavy surf, especially in combination with sand, as well as muddy, quiet water are not tolerated. Increasing surf affects the snail in two different ways: 1. by eliminating the alga species one by one, and 2. by shifting the lower limit of the snail to higher levels. It is shown that surf tolerance may differ from one variety to another, some being rather more tolerant or even "surf loving".

The second part is devoted to the vertical distribution and its causes. This distribution is described both in relation to characteristic tidal levels and to the zones in which particular algae dominate. The average upper limit of the species lies at M.H.W.N. (exceptionally at M.H.W.S.), the average lower limit halfway between M.L.W.S. and E.L.W.S., the optimum level at M.S.L. (for an explanation of abbreviations see p. 37). The lower limit and optimum level of subsp. *littoralis* show a downward trend from the South to the North (see fig. 5). This is probably due to a decrease in salinity towards the North and towards higher levels, perhaps in combination with a decrease in temperature.

After a short and schematic description of the littoral algal zonation in W. Europe the distribution of *L. obtusata* in relation to it is discussed (see tables III–XX and figs. 3 and 4). Apart from its abundance on *Lichina pygmaea* and *Zostera* in (some localities of) England, the snail always prefers *Fucus* and *Ascophyllum*, especially *Fucus vesiculosus*, though in some regions one of the other species *(F. serratus, F. spiralis* or *Ascophyllum nodosum)* may be the most favourite alga. Besides, the snail has been found on *Laminaria saccharina* and—in very small numbers—on *Pelvetia*, *Chondrus*, and a few other algae. Several varieties prefer different Fucaceae and consequently different levels of the intertidal belt. This preference may vary from one region to another, but var. *citrina* prefers *Fucus serratus* (low level) everywhere, var. *olivacea* and *fusca* prefer the algae of the higher levels in all regions.

Experiments showed that *L. obtusata* var. *olivacea* is able to stand at least one month of permanent submergence (much more than the actual maximum in its natural habitat), while the species can stand six days of exposure to the air in a laboratory (which is more than the time of exposure at its average upper limit, but less than that at its absolute upper limit in nature). Probably the former discrepancy is to be explained as the result of negative geotaxis, the latter as due to the protection against desiccation (and rain), offered by the algae: though *obtusata* is the least resistant to drought and fresh water of all *Littorina* species examined, it is found at the same levels as *L. littorea*, but this species does not need algal cover.

Other experiments showed that, even when Fucaceae are not available, no spawning takes place on other algae; some of them, especially *Ulva lactuca*, which is normally avoided, are then eaten by the snail, other algae are not. So Fucaceae are indispensable as a substratum for spawning and much preferred to other algae as food.

After the degree to which the snail can tolerate various abiotic and biotic factors has been examined, the question arises what factors cause the snail to stay within its habitat or to regain it when carried away to deeper water by surf or wave action. Experiments showed that *L. obtusata* has a strong negative geotaxis (cf. table XXII). It is equally strong under water and above water, provided the animals are kept moist; it is not affected by long immersion preceding the experiment; previous emersion perhaps reduces the degree of geotaxis somewhat. Individuals of one variety from different levels on the shore show the same degree of geotaxis (table XXIII), but var. *olivacea* shows stronger geotaxis than var. *citrina*, which lives at a lower level (table XXIV).

The experiments also demonstrated that *L. obtusata* dislikes strong light. This dislike is more pronounced in var. *olivacea* than in var. *citrina*, although light intensity increases with level. However, var. *olivacea* is mostly covered by the algae it lives upon and, therefore, less exposed to light than var. *citrina*, which mainly lives on the surface of the algae.

Both the reaction to gravity and that to light are eliminated by desiccation, which causes the snail to retreat within its shell and to close the mouth of it with the operculum. It was further shown that a thin layer of water, draining away over the animals, may induce them to move downward, following the water. When all algae are removed from the shore, the snails move upward and downward with the tides, though within a range that is smaller than the tidal amplitude. This may be explained as the result of the combined influence of gravity (upward migration), desiccation, light and the effect of draining water (downward migration). In an aquarium with artificial tides and without algae the animals did not show such tidal migrations, but most of them concentrated just above high water mark (see fig. 8). Probably the downward forces were too weak here.

In order to eliminate the abiotic factors, experiments were carried out in which the animals could choose between 8 different algae, all partly immersed and partly uncovered (the 4 Fucaceae, *Chondrus*, *Ulva*, *Porphyra*, and *Gigartina*, see tables XXV–XXX). There was a clear preference for the Fucaceae in all experiments, but a number of snails were also found on the other algae, which are never frequented by them in nature (except *Chondrus*). The preference was most pronounced in var. *olivacea*. Var. *citrina* was always most abundant on *Fucus serratus*, whereas *olivacea* did not clearly show a preference for one Fucacea to others. It further appeared that other Fucaceae were always preferred to the one on which the animals used had been collected.

Both varieties were more abundant on *Fucus spiralis* in the experiments than they are in nature; of var. *olivacea* the same is true with regard to *F. serratus*. These Fucaceae grow at a very high resp. low level of the intertidal belt, somewhat out of the range of the respective varieties. On account of these and other facts it is argued that the distribution of the varieties in nature as regards levels and different algae appears to be caused by 1. attraction of the Fucaceae, 2. the influence of level, 3. wave action.

Next comes the question, how the snails are able to find their favourite algae. VERWEY (table XXXI) proved that they are able to scent them from a distance of 1.5 m. My own experiments showed that taste (table XXXII) and vision (table XXXIII and XXXIV) are not involved in the mechanism that enables the snails to find the right algae. This probably also applies to the tactical sense.

Finally, the combined action of algae and abiotic factors is discussed. EBBINGE WUBBEN proved that *L. obtusata* never leaves tufts of Fucaceae on the shore, except when other tufts are to be found higher up the shore (table XXXVI). The attraction of the algae is the preponderant factor, and it normally outweighs other factors such as gravity, light and the effect of draining water. Upward movements and perhaps tidal migrations may also occur on a shore covered with algae, but only on a small scale and only when a broad belt of algae is present.

In conclusion it may be said that the upper limit of the species (and of var. *olivacea*) appears to be primarily determined by the Fucaceae, and that the same applies to the lower limit, except when surf is strong or when the proper algae extend well into the sublittoral belt. In those cases the lower limit seems to be determined by the combined action of gravity and light. The same applies to the lower limit of var. *citrina*. The upper limit of this variety and the lower one of var. *olivacea*, however, seem to be determined both by their specific preference for different algae and by the immersion-exposure-complex, which influences the snails through its geotaxis, which is stronger in var. *olivacea*.

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Postscript. After this paper went to press my attention was attracted to an article by S. Suzuki on an intertidal species (*Nerita japonica* Dunker), similar in ecology to *Littorina obtusata.* It is therefore interesting to make a comparison between both species. The following notes correspond with references to this Postscript made in the text.

(p. 46, above). The same applies to *Nerita japonica* in Japan, which lives at about H.W.N., though it can stand a submersion in running sea water of 2–3.5 months. This species, too, clearly displays negative geotaxis.

(p. 46, below). *Nerita japonica*, inhabiting the same level as *L. saxatilis*, shows the same drought tolerance (30 days in laboratory conditions).

(p. 49). *Nerita japonica*, which is found at the same level, even cannot stand immersion in fresh water for more than 2 ½ days. This snail, too, lives in a subtropical climate!

(p. 54). In *Nerita japonica*, an intertidal marine Gastropod from Japan, which also shows negative geotaxis as well as negative phototaxis, the latter is able to outbalance the former completely: Suzuki (1934) has demonstrated that the animals will move downward in the light, when the inclination of the surface is 45° or less.

(p. 55). *Nerita japonica*, an intertidal marine Gastropod from Japan, is also directed by draining water, but in an opposite sense: it moves against the water current (Suzuki, 1934). In this species real rheotaxis is involved, since the effect is also to be realised under water. Here rheotaxis generally acts in the same direction as geotaxis, but antagonistic to phototaxis. When both draining water and light act upon the snail, the effect of the latter will outbalance that of the former.

VI. TABLES

TABLE I

Geographical distribution of the colour varieties.

	citrina %	*inversicolor* %	*reticulata* %	*fusca* %	*olivacea* %	*aurantia* %	*zonata* %	*ziczac* %	*rhabdota* %	*alternata* %	*rubens* %	Total number of animals investigated	Ditto during one hou of collecti
S. Brittany	49	2	13	13	20	1	0.5	0.6	—	0.6	0.5	655	164
Isl. of Schouwen.	33	—	—	—	*67*	—	—	—	—	—	—	691	346
Den Helder.	± *76*	0.2	4	—	± 20	—	—	—	—	—	—	865	
N.W. Scotland	17	*4.6*	10.5	*46.5*	18	0.1	0.5	*2.9*	0.2	—	—	881	176
Narvik	19	3.5	16	6.5	*50*	—	2	—	*3*	—	—	200	200

TABLE II

Geographical distribution of the subspecies and form varieties.
(the numbers represent percentages)

	ssp. *typica*	Intermediate forms between the two subspecies	ssp. *littoralis*					
			var. *compacta* + var. *typica*	var. *compacta*	var. *typica*	var. *retusa*	var. *pachychila*	var. *vittata*
S. Brittany	—	—	84.7			*14*	0.3	1
Isl. of Schouwen	—	—	74.6			*17.8*	*7.7*	—
Den Helder	—	—	91.3	7.9	*83.4*	6.8	—	1.9
N.W. Scotland	—	± 2	86.5	*37*	49.5	6	*6*	1.4
Narvik	*4*	*49.5*	46.5	*39.5*	7	—	—	—

TABLE III

Distribution of the species over the algal belts in S. Brittany.

	Quibéron	Kergoff	Total
Fucus serratus	8	131	139
Fucus vesiculosus	37	144	181
Ascophyllum nodosum	35	92	127
Fucus spiralis	*48*	*160*	*208*
Total	128	527	655

TABLE IV

Microdistribution of colour varieties in S. Brittany.

	citrina		*inversicolor*		*reticulata*		*fusca*		*olivacea*		*aurantia*		*zonata*		*ziczac*		*alternata*		*rubens*	
		%		%		%		%		%		%		%		%		%		%
Quibéron	32	25	4	3	4.5	4	8.5	7	74	*58*	—		—		3	2	1	1	1	1
Kergoff	287	*55*	11	2	83	*16*	75	*14*	56	11	6	1	3	0.6	1	0.2	3	0.6	2	0.
Total	319	49	15	2	87.5	13	83.5	13	130	20	6	1	3	0.5	4	0.6	4	0.6	3	0.

TABLE V

Microdistribution of form varieties in S. Brittany.

	typica + compacta		*retusa*		*pachychila*		*vittata*	
		%		%		%		%
Quibéron	123	96	3	2	2	2	—	
Kergoff	427	81	91	*17*	—		9	2
Total	550	84.3	94	14	2	0.3	9	1.4

TABLE VI

Distribution of colour varieties in relation to the algal belts in S. Brittany.

	citrina		*inversicolor*		*reticulata*		*fusca*		*olivacea*		*aurantia*		*zonata*		*ziczac*		*alternata*		*rubens*	
		%		%		%		%		%		%		%		%		%		%
Fucus serratus	*97*	*69*	—		14	10	15	10.7	9	6.4	3	2.1	—		1	0.7	—			
Fucus vesiculosus	*102*	57	4	2.2	25.5	14.2	17.5	9.7	25	13.9	3	1.7	—		3	1.7	1	0.6		
Ascophyllum nodosum	47	37	4	3.1	20	15.7	17	13.4	37	*29.1*	—		1	0.8	—		1	0.8		
Fucus spiralis	73	35.1	7	3.4	28	13.4	*34*	16.3	*59*	*28.3*	—		2	1	—		2	1	3	1.4

TABLE VII

Distribution of form varieties in relation to the algal belts in S. Brittany.

	typica + compacta		*retusa*		*pachychila*		*vittata*	
		%		%		%		%
Fucus serratus	129	92.9	5	3.6	2	1.4	3	2.1
Fucus vesiculosus	159	87.7	21	11.7	—		1	0.6
Ascophyllum nodosum	104	81.9	20	15.7	—		3	2.4
Fucus spiralis	158	76	*48*	*23*	—		2	1

TABLE VIII

Distribution of colour and form varieties in relation to algal belts on the island of Schouwen.

	citrina	*olivacea*	Total	*typica + compacta*	Ad *retusa*	*retusa*	Ad *pachychila*
Fucus serratus	*133*	106	*239*	*183*	13	11	*32*
Fucus vesiculosus	62	121	183	139	20	9	15
Ascophyllum	16	*171*	187	131	*38*	*15*	3
Fucus spiralis	20	62	82	62	10	7	3
Total	231	460	691	515	81	42	53

TABLE IX

Representation of form varieties within the colour varieties at Den Helder.

	typica	Ad *retusa*	*retusa*	(Ad) *compacta*	(Ad) *vittata*
citrina from *F. serratus*	37	—	2	4	—
citrina from *F. vesiculosus*	490	5	—	9	7
olivacea from *F. vesiculosus*	173	23	17	47	9
olivacea from *Ascophyllum*	16	6	6	8	—
Ad *inversicolor* from *F. vesiculosus*	2	—	—	—	—
reticulata from *F. vesiculosus*	4	—	—	—	—
Total	722	34	25	68	16

TABLE X

Distribution of the species over the algal belts in N.W. Scotland.

	Bettyhill, S. exposed bay	Lochinver, N. exposed bay	Lochinver, S. exposed bay	Lochinver, extreme W. point	Average
Laminaria saccharina	20				(20)
Fucus serratus	76	87	*85*		83
Fucus vesiculosus	*182*	*123*	40	74	*105*
Ascophyllum nodosum	Not investigated	41			(41)
Fucus spiralis	74	79			77
Average	88	83	63	(74)	

TABLE XI

Microdistribution of colour varieties in N.W. Scotland.

	citrina		*inversicolor*		*reticulata*		*fusca*		*olivacea*		*aurantia*		*zonata*		*ziczac*		*rhabdota*	
		%		%		%		%		%		%		%		%		%
Bettyhill, S. exposed bay	16	4	2	0.6	23	7	*232*	*67*	69	20	1	0.3	2	0.6	3	1	—	
Lochinver, N. exposed bay	*61*	18	*34*	*10*	19	6	147	45	64	19	—		—		5	2	—	
Lochinver, S. exposed bay	*62*	*50*	—		32	26	9	7	2	2	—		—		*18*	15	—	
Lochinver, extreme W. point	8	11	—		32	*44*	25	34	—		—		4	5	2	3	2	3

TABLE XII

Colour varieties from *Fucus vesiculosus* in N.W. Scotland.

	citrina	*inversicolor*	*reticulata*	*fusca*	*olivacea*	*aurantia*	*zonata*	*ziczac*	*rhabdota*
Bettyhill, S. exposed bay	5	1	15	*128*	32	—	1	2	—
Lochinver, N. exposed bay	6	1	7	78	31	—	—	—	—
Lochinver, S. exposed bay	*19*	—	10	3	—	—	—	6	—
Lochinver, extreme W. point	8	—	*32*	25	—	--	4	2	2

TABLE XIII

Microdistribution of form varieties in N.W. Scotland.

(Increasing surf from top to bottom)

	typica		*compacta*		*retusa*		*pachychila*		*vittata*		Total
		%		%		%		%		%	
Bettyhill, S. exposed bay	133	38	*181*	52	13	4	20	6	1	0.3	348
Lochinver, N. exposed bay	*210*	64	85	25	*30*	*9*	5	2	3	1	333
Lochinver, S. exposed bay	26	21	53	43	3	2	*38*	*31*	3	2	123
Lochinver, extreme W. point	49[1]	67	15[1]	21	2[1]	3	—		*7*[1]	*10*	73

[1] All these animals with very thin, brittle shells, very small.

TABLE XIV

Form varieties from *Fucus vesiculosus* in N.W. Scotland.

	typica	*compacta*	*retusa*	*pachychila*	*vittata*	Total
Bettyhill S. exposed bay	*77*	*87*	8	*11*	1	182
Lochinver, N. exposed bay	*75*	36	12	—	1	123
Lochinver, S. exposed bay	17	17	—	4	—	40
Lochinver, extreme W. point . . .	49	15	2	—	*7*	73

TABLE XV

Distribution of colour varieties in relation to algal belts in N.W. Scotland.

	citrina		*inversicolor*		*reticulata*		*fusca*		*olivacea*		*aurantia*		*zonata*		*ziczac*		*rhabdota*	
		%		%		%		%		%		%		%		%		%
Laminaria saccharina	3	6	—		6	11	30	52	18	31	—		—		—		—	
Fucus serratus	*88*	36	*27*	11	31	12	68	28	12	5	1	0.4	1	0.4	*18*	7	—	
Fucus vesiculosus	29	9	2	0.5	*48*	15	*176*	55	47	15	—		4	1	8	2	2	0.5
Ascophyllum nodosum	36	29	6	5	18	15	33	27	27	23	—		—		3	2	—	
Fucus spiralis	16	5	10	3	6	2	*180*	60	*88*	30	—		—		—		—	
Total	172		45		109		487		192		1		5		29		2	
Total (except *Laminaria*)	169	17	45	4.6	103	10.5	457	46.5	174	18	1	0.1	5	0.5	29	2.9	2	0.2

TABLE XVI

Distribution of form varieties in relation to algal belts in N.W. Scotland.

	typica		*compacta*		*retusa*		*pachychila*		*vittata*	
		%		%		%		%		%
Laminaria saccharina	6	11	51	89	—		—		—	
Fucus serratus	93	38	93	38	11	4	*46*	19	3	1
Fucus vesiculosus	*164*	52	*116*	37	*17*	5.5	11	4	7	2
Ascophyllum nodosum	66	53	46	37	11	10	—		—	
Fucus spiralis	*162*	55	*106*	35	*22*	7	4	1	4	1
Total	491		412		61		61		14	
Total (except *Laminaria*)	485	49.5	361	37	61	6	61	6	14	1.4

TABLE XVII

Distribution of colour varieties in relation to algal belts near Narvik.

	citrina		*inversicolor*		*reticulata*		*fusca*		*olivacea*		*zonata*		*rhabdota*	
		%		%		%		%		%		%		%
Fucus serratus	2	(100)	—		—		—		—		—		—	
Ascophyllum nodosum	6	4.1	4	2.6	*34*	*23.5*	14	9.6	*78*	53.5	4	2.6	6	4.1
Fucus vesiculosus	8	6.2	—		12	9.3	8	6.2	*94*	*73.6*	4	3.1	2	1.6
Fucus spiralis	*60*	*48*	10	8	18	14.4	4	3.1	28	22.4	—		4	3.1
Total	76	19	14	3.5	64	16	26	6.5	200	50	8	2	12	3

TABLE XVIII

Distribution of form varieties in relation to algal belts near Narvik.

	Subsp. littoralis						Subsp. typica						Total
	Var. *typica*		Var. *compacta*		Total		Transitional forms *littoralis-typica*		Pure *typica*		Total		
		%		%		%		%		%		%	
Fucus serratus							2						2
Ascophyllum nodosum	*18*	*12.3*	58	39.7	*76*	*52.0*	66	45.4	4	2.6	70	48.0	146
Fucus vesiculosus	8	6.2	54	42.3	62	*48.5*	62	48.5	4	3.1	66	51.6	128
Fucus spiralis	2	1.6	46	37.1	48	38.7	68	*55.1*	8	*6.2*	76	*61.3*	124
Total	28	7	158	39.5	186	46.5	198	49.5	16	4.0	214	53.5	400

TABLE XIX

Numbers of individuals of *Littorina obtusata* in S. England after data of Colman (1940).

Species	Per kg of alga	Per sq. m
Fucus spiralis	120	4,084
Lichina pygmaea	1,700	
Ascophyllum nodosum	1,410	23,400
Fucus vesiculosus	640	6,400
Fucus serratus	170	1,394

TABLE XX

Numbers of individuals of *Littorina obtusata* in W. Sweden after data of Gislen (1930).

Species	Per kg of alga	Per sq. m	Depth below M.S.L. in cm
Fucus spiralis	16	95	0–30
F. vesiculosus	33	250	0–40
Ascophyllum nodosum	1	14	20–60

TABLE XXI

Mortality of *Littorina obtusata* on different algae. The figures denote numbers. Figures between brackets denote the duration of the experiments in days.

	Fucus serratus		*Ulva lactuca*		*Chondrus crispus*		*Gigartina stellata*	
	total	died	total	died	total	died	total	died
var. *citrina*	49	21 (9)	—	—	50	50 (9)	50	45 (3½)
var. *olivacea*	49	10 (9)	25	3 (7)	41	10 (9)	25	14 (3½)

TABLE XXII

Geotaxis after exsiccation (A) and after immersion (B) (exper. EBBINGE WUBBEN).

I = total number of animals used
II = Number of animals showing negative geotaxis
III = Percentage of animals idem

Treatment before the experiment:	Conditions during the experiment:											
	Immersed						Exposed to the air					
A. Exsiccated during:	Dark			Light			Dark			Light		
	I	II	III	I	II	III	I	II	III	I	II	III
0 hours	58	56	97				18	18	100	18	16	89
6 hours	77	76	99				83	81	98			
18 hours							18	18	100	17	9	53
26 hours	87	86	99				40	35	87	38	28	74
60 hours	41	39	95	40	29	72	19	13	68			
B. Immersed during:												
0 hours	58	56	97				18	18	100	18	16	89
36 hours	77	76	99				83	81	98			
102 hours	46	45	98				40	37	92	41	34	83
160 hours	45	43	96				44	39	89			
250 hours	42	42	100	41	41	100	40	38	95	40	38	95
370 hours	44	42	96				38	37	97	39	34	87

TABLE XXIII

Effect of transposition of animals from different levels. Exper. EBBINGE WUBBEN.

Number of days after the transposition:	Level height in cm	0	1	3	5	7	0	1	3	5	7	0	1	3	5	7	0	2	4	6	9	12	17	0	3	14
MHWS—																										
MHWN—	+ 40—	1)	19	56	56	40	1)	10	36	36	43															
																	D		12	13	19	29	39			
	+ 20—	100	80	38	36	48	100	75	58	53	49	**C**		8	24	38								**E**		
																			4	9	11	13	11			
MSL—	0—		1	6	8	12		15	6	11	8															
																									38	88
MLHWN—																										
MHLWN—																			9	10	17	18	22			
														11	11	19										
	—20—																									
																		15	14	15	15	9	8			
													16	15	29	8										
																		25	18	23	17	9	9		28	6
	- 40—			**A**					**B**																	
												100	84	66	36	35	100	60	43	30	21	21	11	100	34	6
	—60—																									

A and **E**: animals from a high level
B and **C**: animals from a low level
D: as **A** and **E**, but kept in a cage at low level during a month

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1) In this belt only a scarce algal cover was present (*Fucus spiralis*)

TABLE XXIV

Results of movement of *Littorina obtusata* due to negative geotaxis. Start: under water. Figures denote numbers of animals.

	After 15 hours		After 84 hours	
	olivacea	*citrina*	*olivacea*	*citrina*
Above water	132	88	134	48
At the surface	1	8	4	9
Below water	11	4	15	27

TABLE XXV

Numbers of animals used in experiments 1–7.

Exp. no.	Duration of exp. in days	Var. citrina From *F. serratus*	Var. citrina From *F. vesiculosus*	Var. olivacea From *F. vesiculosus*	Var. olivacea From *Ascophyllum*
1	3.5				109
2	4.8				88
3	3	93			
4	6	215			211
5	7	222			210
6	5		306	300	
7	6.5		277	283	
8	5	68			87
9	2		197	157	
Total		598	780	740	705
		1378		1445	
		2823			

TABLE XXVI

Choice of algae by var. *olivacea* (exp. 1–7).

Number of exp.	From *Ascophyllum* 1	2	4	5	total	From *F. vesiculosus* 6	7	total	Total	
Fucus vesiculosus	*19*	*27*	33	18	*97*	31	8	39	136	613.
Fucus spiralis	14	15	22	*37*	*88*	26	*68*	*94*	*182*	
Fucus serratus	13	16	13	28	70	34	34	68	138	
Ascophyllum	3	8	*44*	9	64	*66*	27	*93*	157	
Ulva	5	0	7	3	15	5	14	19	34	93.
Porphyra	2	0	1	3	6	8	12	20	26	
Chondrus	1	1	2	1	5	9	4	13	18	
Gigartina	0	2	1	2	5	5	5	10	15	

TABLE XXVII
Choice of algae by var. *citrina* (exp. 1–7).

Experiment no.	From *Fucus serratus*				From *F. vesiculosus*			Total	
	3	4	5	Total	6	7	Total		
Fucus serratus	*11*	*34*	*36*	*81*	*33*	*37*	*70*	*151*	463
Fucus vesiculosus	9	*35*	24	68	*32*	14	46	114	
Fucus spiralis	5	26	25	55	*29*	*40*	*69*	124	
Ascophyllum	7	21	4	32	*33*	9	42	74	
Chondrus	6	16	4	26	25	8	33	59	162
Ulva	*11*	2	11	24	14	9	23	47	
Gigartina	4	5	4	13	8	4	12	25	
Porphyra	3	3	1	7	16	8	24	31	

TABLE XXVIII
Results of exp. 1–7 after correction.

	olivacea	*citrina*	Total
Ascophyllum	*193*	142	*335*
Fucus vesiculosus	175	134	309
F. serratus	120	*163*	283
F. spiralis	120	102	222

TABLE XXIX
Result of exp. 9.

	olivacea	*citrina*	Total
F. serratus	*38*	*57*	*95*
Ascophyllum	25	32	57
F. spiralis	25	27	52
F. vesiculosus	9	9	18
Total	97	125	222

TABLE XXX
Total of exp. 1–7. Numbers of animals on algae above water surface (var. *olivacea*).

Experiment no.	1	2	4	5	6	7	Total
Fucus serratus	7	*15*	2	19	28	17	88
Ascophyllum	3	8	*14*	4	*46*	12	87
Fucus spiralis	9	13	13	*25*	17	*44*	*121*
Fucus vesiculosus	*17*	12	7	9	10	4	59

TABLE XXXI

Numbers and percentages of *Littorina obtusata* attracted by Fucaceae from a distance of 1.5 m in flowing water. Experiments VERWEY. For explanation see text.

Experiments without algae			Experiments with algae			
Date	Not around inflow	Around inflow	Date	Not around inflow	Around inflow not on algae	Around inflow on algae
22 X	115	36	21 X	164	6	± 25
27 X	185	6	22 X	139	8	62
2 XI	180	3	29 X	132	20	38
5 XI	148	6	3 XI	138	23	16
18 XI	125	1	6 XI	111	21	30
23 XI	112	4	19 XI	112	9	9
25 XI	102	10	24 XI	108	5	18
			26 XI	121	4	3
Total	852	30	Total		96	± 201
Percent.	96.5	3.5				
			Totals	1025	297	
			Percent.	78	22	

TABLE XXXII

Choice between algal extracts.

	olivacea				*citrina*				Total
Experiment no.	12	13	14	Total	12	13	14	Total	
Ascophyllum	5	9	13	27	7	*7*	18	32	59
Fucus vesiculosus	0	*10*	11	21	4	4	31	39	60
Fucus serratus	*12*	6	3	21	*17*	6	13	36	57
Fucus spiralis	11	1	—	18	6	3	—	14	32
Chondrus	5	3	4	12	10	2	7	19	31
Ulva	10	8	*14*	32	12	*7*	*39*	*58*	*90*
Porphyra	6	*10*	9	25	12	6	31	49	*74*
Gigartina	7	5	3	15	10	4	15	29	44
Average number on the check plates	0.5	2 8	6	11.5	3.5	5 5	14	22.5	33.5

TABLE XXXIII

Choice of *Littorina obtusata* of different species of algae (experiment in complete darkness). Figures denote numbers of animals.

	var. *olivacea*	var. *citrina*	Total
Fucus vesiculosus	17	5	60
Ascophyllum nodosum	13	4	
Fucus serratus	12	9	
Chondrus crispus	5	1	15
Ulva lactuca	2	1	
Gigartina stellata	1	3	
Porphyra laciniata	0	2	
Average of the check tiles without algae . . .	2	1	3

TABLE XXXIV

Choice of *Littorina obtusata* of different sectors containing different species of algae under glass. Figures denote numbers of animals.

		olivacea	*citrina*
Less illuminated sectors	*Gigartina*	13	21
	Fucus serratus	10	12
Intermediate sectors	*Ulva*	6	5
	Empty	5	2
Bright sectors	*Ascophyllum*	0	1
	Chondrus	0	2

TABLE XXXV

Behaviour of animals on a shore without algae. Exper. EBBINGE WUBBEN. The lowermost belt was covered with algae; for explanation see text.

Tidal level	Level height in cm								
Days after start		0	1	2	3	4	5	6	7
MEHWS—									
	100—		1	1	1	1	0	0	0
	80—		33	26	25	7	0	1	2
	60—								
MHWS—			30	22	9	17	13	7	5
MHWN—	40—								
	20—		21	24	10	18	14	7	4
MSL—	0—	215	35	60	37	19	15	12	6
MLHWN—									
MHLWN—	—20—		30	14	12	3	4	3	5
Total		215	150	147	94	65	46	30	22

TABLE XXXVI

Influence of algae on negative geotaxis (exper. EBBINGE WUBBEN).

Tidal level	Level height in cm	With algae		Without algae	
		After		After	
		0 day	1 day	0 day	1 day
MHWS					
MHWN	+40				
					1
	+20				
					0
MSL	+0				
MLHWN					3
MHLWN					
					8
	−20				
					14
	−40				
		50	22	50	9
	−60				
			3		
MLWN					1
MLWS	−80				

OBSERVATIONS ON THE STRAINING OF SUSPENSIONS BY MUSSELS

by

P. M. L. TAMMES and A. D. G. DRAL

(Zoological Station, Den Helder)

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I. INTRODUCTION

This paper deals with the question what percentage mussels retain from the material suspended in the water they pump over and through their gills, and what influence the size of the particles of the suspended material has on the percentage retained. The question has given rise to a good deal of controversy.

The gills of mussels consist of a double wall of loose filaments, connected at intervals by ciliar discs. Between these filaments there are openings, the so-called ostia (fig. 1).

The water is transported through these ostia by a ciliary mechanism, and at the same time particles are strained off. After that the water passes through the intra-filamental chamber to the suprabranchial chamber and further to the exhalent aperture.

Four groups of cilia are found (fig. 1):

a. the frontal cilia, on the front side of the filaments;

b. the large latero-frontal cilia, neatly arranged in a row along either side of the frontal edge; in cross sections only one of these cilia is visible on each side; the cilia from both sides of the ostium interlock;

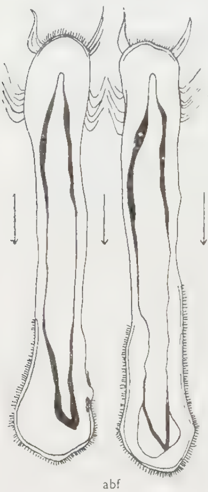

Fig. 1. Two filaments of the gill of a mussel, with the ostial opening between them and the ciliar groups as indicated in the text. Watercurrents in the direction of the arrows. abf = abfrontal side. After D. Atkins, Journ. Mar. Biol. Ass., **17**, 489–543, 1931, somewhat changed.

c. the lateral cilia, in the ostia not far from the latero-frontals;

d. the abfrontal cilia.

The lateral cilia, and perhaps also the abfrontal cilia, take care of the water transport, i.e. the pumping. The first two groups deal with the straining.

The classic opinion on this straining is that the laterofrontal cilia form a sieve. Particles would be sieved out and thrown onto the frontal cilia. Embedded in mucus they are then transported by the frontal cilia to the foodgroove. Already in 1905, however, Wallengren observed that the particles may adhere to the long latero-frontal cilia, which are very sticky. This does not point to a sieve mechanism.

In 1941 MacGinitie suggested that an altogether different mechanism might be involved. According to his theory, a sheet of mucus is secreted which covers the whole gill surface, and the straining process is supposed to consist in the filtering of water through this sheet. Such a film of mucus would be able to strain out very fine particles and colloidal matter completely by ultra-filtration. If no mucus sheet were secreted, the particles of average size would pass the gills, and only very large ones that cannot pass the ostia would be sieved out. MacGinitie actually observed that the secretion of mucus can be stopped in mussels. The mechanism itself, however, was not studied in mussels, but in the

Gephyrean worm *Urechis*, which makes a mucus feeding net. In his experiments with proteins he came to the conclusion that the pores in the mucus net of *Urechis* were between 3 Å and 90 Å (average 40 Å). If the same is assumed for mussels, all particles above 90 Å would be filtered out in one passage when a mussel is feeding.

The use of mucus feeding nets is actually found in other molluscs. Werner (1951) has described two filiform mucus feeding nets in the Gastropod *Crepidula.* One net is spun behind the inhalent aperture by a mantle gland. It removes the larger particles. The other consists of threads that are parallel to the filaments of the gills and are transported over the gills by cilia.

The view that very small particles, down to colloids, would be retained, was already held by Fox, Sverdrup, and Cunningham (1937), and in 1943 Fox and Coe made reference to some preliminary experiments with colloids, such as congo red and soluble starch, which showed that both substances were retained.

Galtsoff and Loosanoff determined the extent of straining in oysters by comparing the inhaled water with the exhaled. To this end they brought a tube into the exhalent aperture, so that the water could be caught. They found that the extent to which small particles are strained out may vary considerably. MacGinitie's hypothesis might be able to account for this, and several investigators defended his view.

In our own experiments we placed a tube in the exhalent aperture of mussels, in the same way as Galtsoff and Loosanoff did with oysters. The extent of straining was studied by comparing the turbidity of the water leaving the animals with that of the inhaled water. The results differed from what might be expected of the action of a sieve or ultra-sieve mechanism, and rather suggested another mechanism. Direct observations on very young mussels, where it is possible to look right through the shells with a microscope, confirmed this view. They suggested a mechanism in which particles are caught by contact with adhesive substances, as was described by Wallengren. The particles adhere to the single latero-frontal cilia and are then wiped off on to the frontal cilia.

In working with different suspensions the relation between the size of the particles and the extent of straining was studied, and different size groups were distinguished. In some size-groups variations in the extent of straining were considerable and appeared not to be directly related to the rate of pumping. In comparing the results especially the maximum percentage of straining was considered important.

The experiments were carried out from February to September 1952 at the Zoological Station in Den Helder, Holland. We are indebted to the director, Dr. J. Verwey, for his suggestions and helpful criticism, and to Dr. P. Korringa for his critical reading of the manuscript.

II. MATERIAL AND METHODS

The experiments were carried out with common mussels *(Mytilus edulis)* of 6–7 cm length from the neighbourhood of Den Helder. Before use the mussels were kept for a couple of days in running water. The fairly clear seawater of the Station was used for this purpose.

The method employed to study the extent of straining was based on a comparison of the inhalation and exhalation water. Inflow and outflow had therefore to be separated. To this end a small plastic tube was inserted into the exhalent aperture. A small part of the shell in the neighbourhood of the latter was ground away, the shells were then carefully forced open with a forceps, and the plastic tube was inserted into the aperture. The outer diameter of the tube was 4, the inner 2 mm. The inserted end of the tube was cut off at an angle of 45° (fig. 2) to make it fit properly into the cavity. The mussel was then embedded in plaster of paris in such a way that a space was left open for the inflow of water.

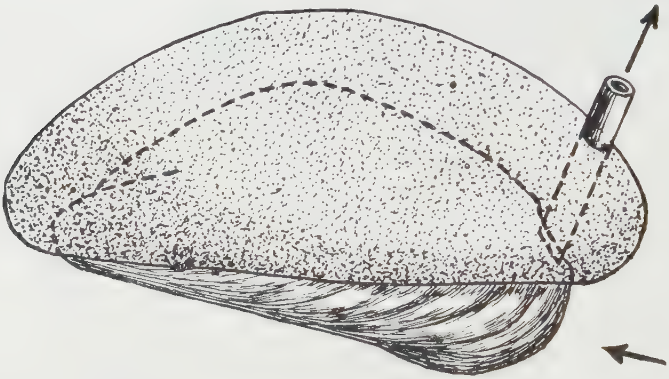

Fig. 2. Mussel in plaster of paris, see text.

The specimens would be prepared in the afternoon and used during the following days. They do not keep well for a long time because the plaster dissolves in seawater. The preparation did not always succeed and a number of mussels had to be discarded next morning. The mussels were tested before use by placing a small drop of a carmine suspension with a pipette in front of the opening of the tube. If this suspension was blown away by a jet of water the mussel was supposed to be suitable for the experiment.

The mussels, thus prepared, were placed in an aquarium in which the water level was kept constant by overflow (fig. 3). The apparatus allowed of electrical regulation by means of a contact thermometer (a), a relais (b) and an electric heater (c). A large cylinder jar (d) with ice and salt for cooling could be placed in the basin, which further contained a tube for aeration and stirring (e). A plastic tube was attached by means of a rubber connection to the plastic tube inserted into the mussel siphon (f). This tube, carrying off the outflowing water, as well as a control tube (g) placed beside it, were bent over the side of the aquarium. In order to prevent any siphonal action or extra-pressure the ends of both tubes f and g were fixed at exactly the same level as the water level in the mussel's aquarium. The water dripping from tube f must therefore have been pumped by the mussel.

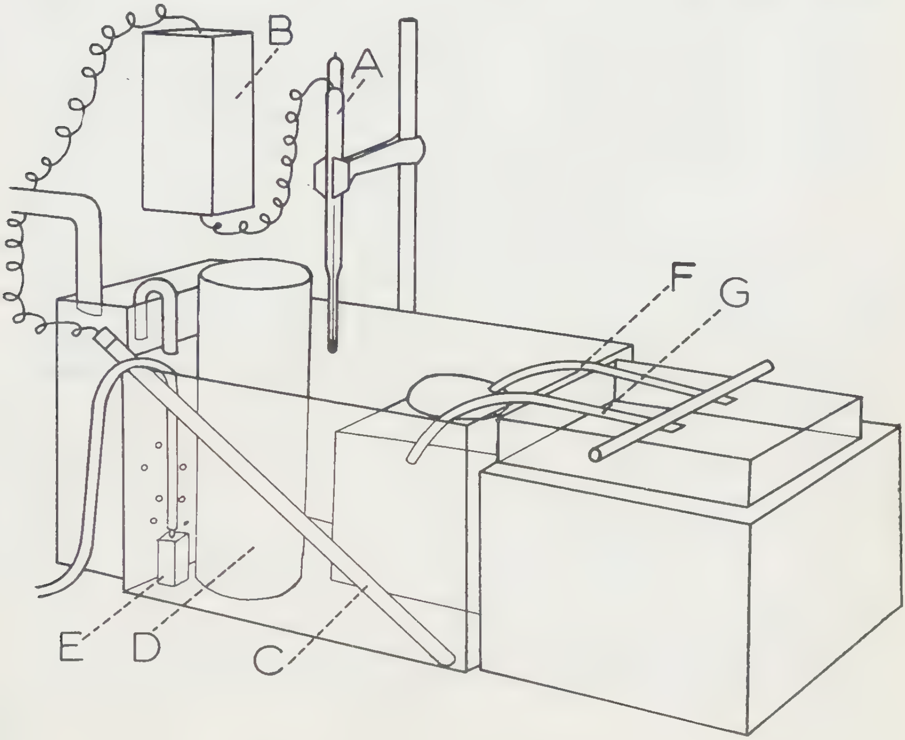

Fig. 3. Apparatus used, see text.

The amount of exhaled water was measured in two ways:

a. over a short time range by recording the time intervals between subsequent drops;
b. over a long time range by recording the time needed for filling a small cuvette.

The outgoing water was collected in a small cuvette and then compared with a sample of the original water taken from near the inhalent aperture. The concentration of the suspensions was determined by means of an electrical colorimeter, trademark "Objecta", supplied by Bleeker, Holland. The quantities of light transmitted are a measure for the concentration of the suspensions; the extinction values were used as such. The colorimeter has a monochromator and the determinations were made in violet light of 4200 Å. The percentage strained can be determined from the extinction values found, since it is:

$$100 \times \frac{\text{Extinction initial water minus extinction exhaled water}}{\text{Extinction initial water}}$$

In the preparation of suspensions substances should be used which settle slowly, have a particle size as homogeneous as possible, which do not quickly flocculate in seawater and are easily suspended. Further, the particles must not disintegrate during straining. In our experiments we used the following suspensions, the particle sizes of which are given in microns.

carbon black	0.01–0.3
milk (fresh)	0.14–6.3
bacteria	(0.4–0.6) × (2–3)
flagellates	1.5–2.5
beaten cowblood	7–8
bolus alba (clay)	up to 15 (after one night settling)
maize starch	2–35
wheat starch	2–37
Lycopodium powder	30–40
silt suspension	up to 40 (after 1–2 hrs settling)

III. PUMPING

The pressure produced by the mussel's pumping was determined by comparing the height of the water pressed into an extension piece of the plastic exhalation siphon with the waterlevel within a control tube of the same diameter, placed in the water beside the mussel. The results obtained are given in the following table.

TABLE I

Pumping pressure of mussels of 6–7 cm length.

Date (1952)	Temp. °C.	Rate of pumting in cc/hr	Pressure in mm of water
4–4	13	120	4
5–4	14	150	5
5–4	9	222	5·5
9–4	9	195	5
24–4	18	150	3
24–4	18	200	3

The highest pressure found was only 5.5 mm of water. Though it should be realized that, if a mussel has no tube in its exhalation siphon, the pressure obtained may be higher, it is probable that the pumping mechanism produces only very low pressures. This seems surprising in view of the fact that rather strong currents may be observed in front of the exhalent aperture of pumping mussels, especially in large specimens. One can easily demonstrate, however, by connecting two aquaria with a difference in level of about 5 mm, by means of a narrow siphon filled with carmine suspension, that very small differences in pressure may cause rather strong currents.

The quantities of water pumped were determined by recording the amount of time elapsing between drops. The seawater used was nearly free of suspension. The drops were about 0.05 cc each. The quantities pumped by such harnessed mussels are much smaller than those pumped by normal animals owing to the resistance in the tube. In a number of cases a fairly constant rate of pumping was observed, interrupted by shorter or longer periods of rest. Such periods may also be observed in normal mussels, but WALLENGREN (1905) has shown that pumping is continuous under normal conditions, and that changes or periods of rest are due to external influences. The periods of rest continued when a tube was inserted between the mantle edges and one would therefore feel inclined to ascribe them to a ciliary standstill. Very regular pumping with few periods of rest was observed when the temperature was lowered after it had been high (20–27 °C) for some time. High temperatures themselves produced a higher frequency of the periods of rest.

In fig. 4 a graphic representation is given of observations made on

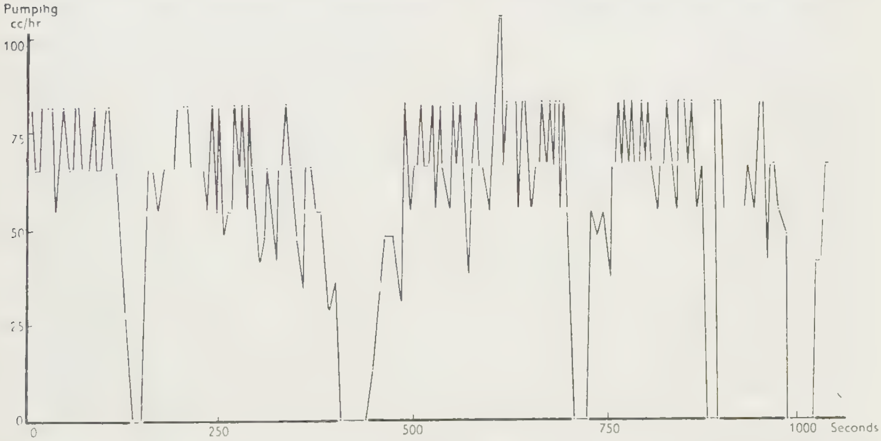

Fig. 4. Graphic representation of the mussel's pumping, measured by recording intervals between drops. Results expressed in cc per hour. Short periods of rest are clearly noticeable. See text.

the quantity of water pumped by one particular mussel. For a period of 1000 seconds the number of seconds between successive drops was counted and the results expressed in terms of cc per hour. Accordingly, there are a number of levels corresponding with the numbers of seconds. All volumes in between the levels would have been present if parts of seconds had been recorded. Actually, the variation of pumping will have been more gradual than indicated by the graph.

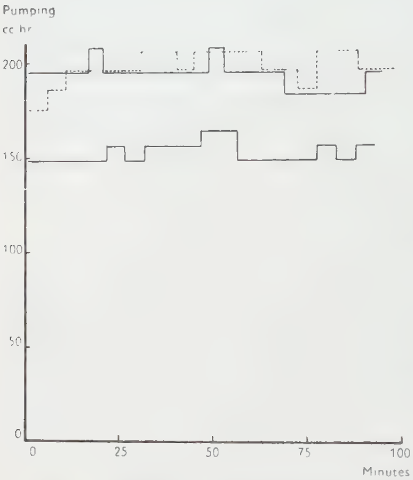

Fig. 5. Graphic representation of the mussel's pumping, measured by noting the time needed to pump 13 cc. Results for 3 specimens expressed in cc per hour. Short periods of rest escape observation.

Observations over somewhat longer periods were made by means of small cuvettes of 13 cc. The time required for a mussel to fill a cuvette was recorded. By this method more average values were obtained (fig. 5). Because of their short duration, periods of rest now escaped observation. Changes in the quantities of water pumped would only be observed after a continued or stronger decrease in pumping or after longer periods of rest.

The results given in figs. 4 and 5 were obtained with mussels kept in seawater from the Station's circulation system, which contains very little suspended matter. If similar observations are made on mussels in seawater containing more material in suspension, the mussel's water output may decrease considerably, as follows from table II.

In view of the fact that pumping may show much variation, the number of observations is in some cases small, but the results tend to show a decrease in the quantities of water pumped with an increase in the concentration of the suspension. This decrease is not due to an increase in the periods of rest, as was proved by timing intervals between drops. The results agree with those of Loosanoff and Engle (1947) and Loosanoff and Tommers (1948), who found for *Ostrea virginica* that an increase in the concentration of organisms, silt, kaolin, $CaCO_3$ and Fuller's earth causes a reduction in the quantities of water pumped of up to 80% and more.

Observations were also made on the influence of temperature on the quantity of water pumped. These observations will be published elsewhere, however.

TABLE II

Average quantities of water pumped at different concentrations given in sequence of experiments and expressed in cc per hour. Numbers of observations between brackets.

Mussel number	Clear water	Milk	Low conc.	High conc.	Clear seawater	Low conc.
I	195 (8)		160 (9)	112 (24)	156 (11)	122 (8)
II	177 (10)		148 (7)	134 (30)	209 (10)	190 (5)
III	220 (9)		205 (17)	122 (21)	183 (8)	176 (6)
IV	146 (6)		150 (13)	93 (19)	175 (8)	170 (6)
Average	185		166	115	181	165
V	104 (7)	Blood	46 (4)	53 (9)	81 (5)	81 (3)
VI	98 (6)		100 (8)	86 (15)	147 (9)	123 (4)
Average	101		73	70	114	102
VII	188 (6)	Silt	136 (5)	120 (4)	173 (14)	145 (11)
VIII	208 (7)		196 (7)	148 (12)	223 (7)	186 (5)
IX	62 (2)		75 (3)	72 (7)	101 (4)	77 (3)
Average	153		136	113	166	134

IV. STRAINING OF SUSPENSIONS IN RELATION TO PARTICLE SIZE

A. STRAINING OF SUSPENSIONS OF A SINGLE SUBSTANCE

The water pumped through the gills of a mussel is strained. The particles retained are either used as food or discarded as pseudo-faeces. Very fine particles can be strained out, and it is known that mussels can even clear bacterial suspensions. ZOBELL and FELTHAN (1938) showed that the animals can live for long periods on nothing but bacteria and, as has been stated in the Introduction, even colloids are supposed to be retained. In the experiments in question, however, the same water was pumped again and again through the mussels and it is uncertain what percentage of the material was strained out in a single passage.

As described in section 2, the percentage retention of a given material was found by comparing the initial concentration with the concentration of the exhaled water. The colorimeter made a rapid determination of both concentrations, expressed in extinction values, possible, and from these values the straining percentages were directly calculated in accordance with the formula given on page 92.

A number of preliminary experiments were carried out with suspensions of beaten cow blood in seawater. It was found that the percentage of material retained would show a great deal of variation in one and the same animal, even when pumping was constant. Since this could not hold for particles too large to pass the ostia, we supposed that there might be different size groups of particles, each behaving differently. Their percentage retention might depend on the diameter of the ostia on the one hand, on the spaces between the latero-frontal cilia on the other. Accordingly, we worked with particles of very different sizes.

1. A group of large particles, of such a size that they would not be able to pass the ostia, which have a diameter of some 40–45 μ. We chose *Lycopodium* spores as a representative of this group.
2. A group of medium particles, which could pass the ostia, but would at the same time be larger than the spaces between the latero-frontal cilia, so that they could probably be completely retained. Blood appeared to be a representative of this group; starch grains of wheat and maize might likewise be.
3. A group of small particles, possibly too small to be well retained. In this size group experiments were made with milk, flagellates, bacteria, carbon black, and colloids.

The suspensions are here dealt with in order of particle size.

1. *Lycopodium spores*

The largest particles of uniform size were the spores of *Lycopodium*, which can be had as *Lycopodium* powder from druggists or chemists. They form an ideal material for experiments like these, since they are rather uniform in size: about 30–40 μ; they are light, do not flocculate, and easily disperse in seawater. In all, we obtained 90 values for the extent of straining measured in 4 animals. Each value was obtained by determining both the extinction value of the exhaled water in a cuvette of 1fi cc and the extinction value of the suspension at the start in such a cuvette. As stated above, the straining percentages were calculated directly from these two in accordance with the formula given on page 92.

It follows from these observations that 93–100 % of the *Lycopodium* spores are retained. Microscopic examination of the exhaled water revealed the presence of spores of normal size. Their number, however, was too small to exert any influence on the colorimetric determination in those cases where the percentage of straining was 100.

2. *Oil-emulsion*

A suspension containing even larger particles than *Lycopodium* spores, but at the same time containing a high percentage of very small particles, was an oil emulsion in milk. It was prepared by thoroughly mixing 75 cc of seawater with 25 cc of fresh cow milk, 5 cc of peanut-oil and 4 drops of an emulgator (synthetic detergent). This mixture was added to 10 litres of seawater. The oildrops have various diameters, up to 165 μ, the majority were 30–50 μ, the milk globules are for the greater part below 1 μ.

Since the particles showed so much variation in size it was deemed of interest to observe whether after filtration a difference in diameter could be noted. To this end the largest particles contained in the exhaled water of 3 different mussels were measured and found to be 15, 12 and 6 μ respectively. At the start of another experiment the largest particles of the suspension were found to be 70 μ. In this case the exhaled water of a mussel was studied 3 times. In all, 20 oil drops were counted and found to measure 6–15 μ, the majority being about 10 μ. This means that, relatively, more large drops are retained than small ones.

3. *Wheat starch*

A number of experiments were carried out with wheat starch. The grains differ much in size, from about 2 to 37 μ. They are heavy and therefore settle rapidly. To make sure that no values would be found for the extent of straining that were actually too high because the grains might possibly settle within the mussel, an empty mussel shell in which a tube had been fastened was used by way of control. The tube was fitted in such a way that by siphonic action the same flow of water was obtained as in the living mussels. Straining values were determined 3 times.

Again, the difference in diameter between the grains present at the start and in the exhaled water was determined. To this end, both from the water that passed the empty mussel and from the water exhaled by the living mussel 100 grains each were measured and their sizes compared.

TABLE III

Rates of pumping and extent of straining for wheat starch. Diameter of starch grains in exhaled water and control. All dimensions in microns, each sample 100 grains measured.

Pumping (cc/hr)	Straining (%)	Diameters			
		Average grain size control	Average grain size exhaled water	Diff.	Mean error of diff.
130	73	9.8	5.2	4.6	0.7
130	85	11.3	5.3	6.0	0.7
104	81	8.1	5.6	2.5	0.6

It follows from fig. 6 and table III that in 3 cases (one cuvette filled in each) percentages of straining of 73, 81, and 85 were obtained. The averages for 100 grains measured, the differences between them, and their mean errors are also given in table III. Relatively, the small grains have increased in number, the large grains have decreased. The decrease in average grain size is significant. Larger grains are better retained than small ones.

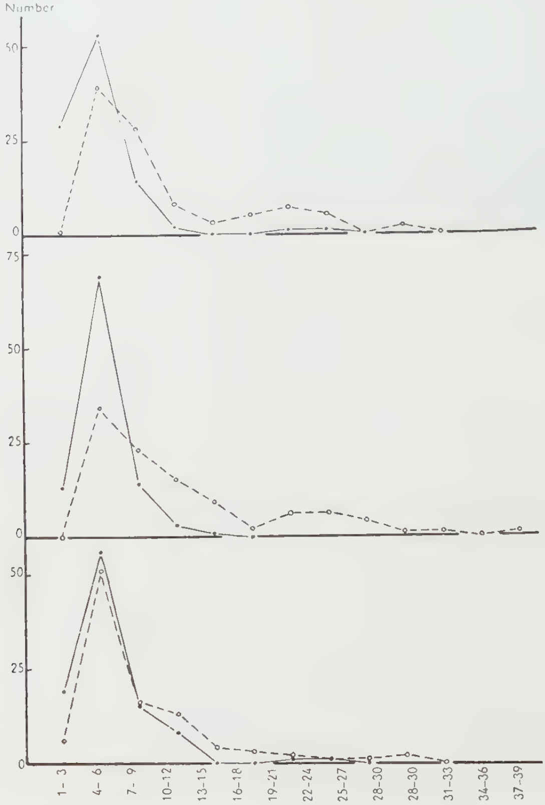

Fig. 6. Differences observed in the size of grains of wheat starch after passage through mussels. Continuous line refers to exhaled, dotted line to control water. Each sample 100 grains measured. Sizes in microns.

4. *Maize starch*

Grains of maize starch, like those of wheat starch, vary a good deal in size, from about 2 to 35 μ diameter, but grains above 30 μ hardly occur.

The method employed was the same as in the case of wheat starch, an empty mussel shell being used as control. Here, again, 3 values (relating to one cuvette each) were obtained for the extent of straining, and in each case, both from the exhaled water and the control, 100 grains were measured and their sizes compared. It was difficult to find

100 grains in those cases in which straining had been to the extent of 100%. The figures are given in table IV and fig. 7.

TABLE IV

Rates of pumping and the extents of straining for maize starch. Diameter of starch grains in exhaled water and control. All dimensions in microns, each sample 100 grains measured.

Pumping (cc/hr)	Straining (%)	Diameters			
		Average grain size control	Average grain size exhaled water	Diff.	Mean error of diff.
97	75	8.8	7.1	1.7	0.4
88	± 100	11.6	9.4	2.2	0.7
82	± 100	10.4	5.7	4.7	0.7

It follows from fig. 7 and table IV that the extent of straining amounted to 75, 100, and 100% respectively and that, here again, larger grains are better retained than small ones. Relatively, the small ones increase in numbers. The decrease in average grain size is significant.

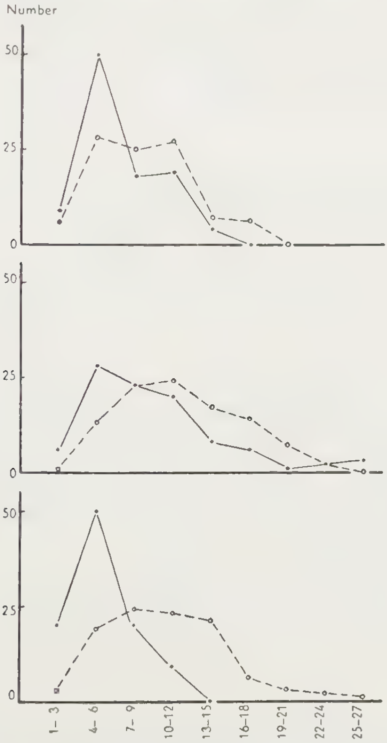

Fig. 7. Differences observed in the size of grains of maize starch after filtration. For explanation see fig. 6.

5. *Blood*

Many experiments were carried out with fresh, beaten cow blood, obtained from the slaughter house and kept fresh for several days on ice. It seemed ideal because it produces a homogeneous suspension of uniform particle size (7–8 μ) and keeps well in seawater. Sedimentation of this suspension is low as compared with others. The concentration used was always 0.17 cc of blood per litre of seawater (extinction value ± 0.250). The results of the experiments are summarized in fig. 8.

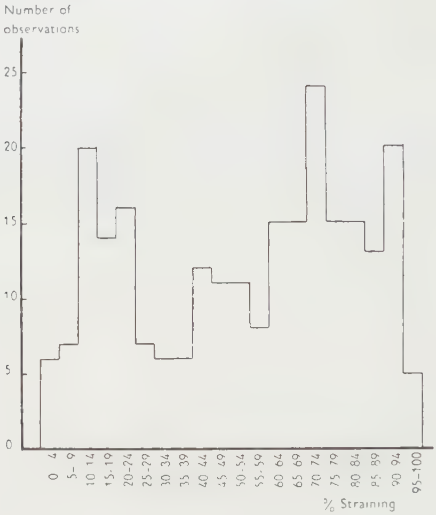

Fig. 8. Frequency distribution of values found for the extent of straining of blood suspensions of 2 cc per 12 litres. All results obtained with 5 animals added up.

It follows from these results that the extent of straining may attain a value of 98 %. The most striking result with blood was, however, the pronounced variation in the extent of straining in one and the same animal combined with constant pumping. There were periods when nearly everything was strained out, at other times nearly everything was let through (see fig. 9).

No relation was found between the rate of pumping and the extent of straining. These results are in agreement with those of Loosanoff and Engle (1947), who found much variation in straining in oysters.

6. *Milk*

Milk is an emulsion of particles of different sizes, varying in fresh milk from 0.14 to 6.3 μ. The majority are smaller than 1 μ. About 10 cc of milk were used per 12 litres of seawater. The results are given in fig. 10.

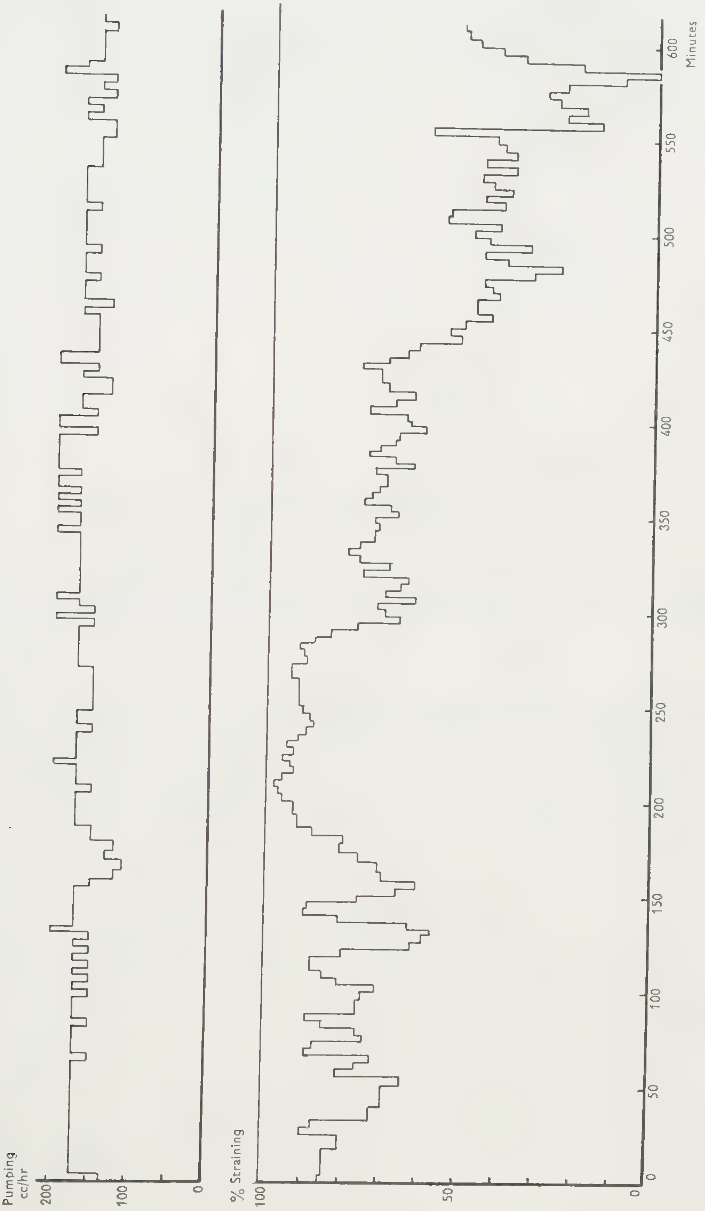

Fig. 9. Quantities of water pumped and percentages of blood strained from a suspension of 2 cc blood per 12 litres of seawater. The extent of straining changes continually, also when pumping is more or less constant.

Fig. 10 shows that the extent of straining varies between 5 and 60 %. A value of 60 %, however, is apparently only attained with difficulty, most values are 5–20 % only. Mussels, therefore, retain only a small part of the particles of such a suspension in one passage.

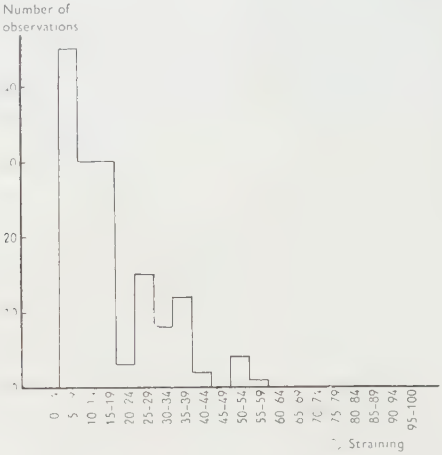

Fig. 10. Frequency distribution of values found for the extent of straining of milk suspensions of 10 cc per 12 litres. All results obtained with 9 animals added up.

In milk, as in starch, larger particles are strained out better than small ones. Since the size of the particles, especially the small ones, was too small to be measured directly, an optical method was employed, based on the principle that the difference in scattering light of different wave lengths increases when the particles causing this scattering become smaller.

Light, falling through a suspension, is scattered. Scattering depends on the number and size of the particles, the difference in refractory index between medium and particles, and the wave length of the light. If the particles are not very small (above about 10 μ) scattering is the same in light of different wave lengths. If the particles become smaller, scattering becomes different in different wave lengths, till below a particle size of 0.1 μ (1000 Å) scattering is inversely proportional to the fourth power of the wave length (Lord Raleigh). The more the light is scattered the higher the extinction value recorded by a colorimeter. Therefore, the smaller the particles of a suspension the larger the relative difference between the extinction values in light of different wave lengths, e.g., violet and red. If a suspension contains enough particles of a size below 1 μ, a mussel straining off more large than small particles will cause the average particle size to diminish and the difference between the extinction values for, e.g., red and violet light in a colorimeter to increase. It should be added that dilution of a suspension does *not* cause any change in the relative extinction values for red and violet light in a colorimeter.

The results are given in table v. The colorimeter readings before and after filtration as well as the straining percentages calculated from them are given for the violet and red part of the spectrum (4200 and 7000 Å).

TABLE V

Extent of straining of fresh cow milk, measured in violet and red light.

	Colour of light	
	Violet, 4200 Å	Red, 7000 Å
Colorimeter extinction		
Initial value:		
I	0.260	0.110
II	0.285	0.115
III	0.280	0.105
IV	0.280	0.105
Exhaled water:		
I	0.160	0.050
II	0.220	0.065
III	0.200	0.055
IV	0.190	0.052
Percent. of straining:		
I	40	55
II	23	42
III	29	48
IV	32	51

Centrifuged milk was also used. Centrifuging was performed at 3500 revolutions a minute for 45 minutes. Since it may be expected that in such a suspension only particles of small size are found the difference in the extent of straining, when measured in red and violet light, must be greater. A comparison of tables V and VI shows that this is indeed the case.

TABLE VI

Extent of straining of centrifuged cow milk, measured in violet and red light.

	Colour of light	
	Violet, 4200 Å	Red, 7000 Å
Colorimeter extinction		
Initial value	0.080	0.015
Exhaled water	0.070	0.010
Percent. of straining	12.5	44

7. *Clay (bolus alba)*

A result similar to that with milk was obtained with a suspension of clay (bolus alba), which was used after the large particles had settled by standing overnight in seawater. The straining percentages for a mussel in this suspension were 75 in violet and 93 in red light. Again, the larger particles were strained out better than the small ones.

8. *Flagellates*

A small number of observations were carried out on the straining of flagellates. For this purpose Mr. J. W. DE BLOK kindly provided the material. The length of the flagellates was 1.5–2.5 μ. The values found (19 in all) relate to one and the same mussel. The extent of straining varied between 0 and 50% (both values attained once), with 17 values in between.

9. *Bacteria*

Suspensions of bacteria were made by adding sugar and ammonium phosphate to seawater. After a few days a rich bacterial suspension would develop, which could be diluted for our purpose. We thus had material with a particle size of 0.5–2.5 μ at our disposal. The extreme values found for the extent of straining were 5 and 24%. Since only 10 observations (on 2 animals) were made, these extremes are not of much value.

Low values for the straining of bacteria are well in line with the findings of GALTSOFF (1928) that oysters keep back only a small fraction of *Bacterium coli* added to the water; 70–90% escaped through the gills and could be recovered in the exhaled water.

10. *Carbon black*

Suspensions of carbon black were made by diluting Chinese ink with seawater. Its particle size is very small. The largest particles can only be seen with the aid of an oil-immersion objective. According to VAN DER WAARDEN (1950) the size of the particles is between 10 and 300 mμ (100-3000 Å). We used 0.5 cc of Chinese ink per 10 litres of seawater. The suspension keeps well for a couple of hours, but flocculates afterwards. In all, 10 values were obtained (for 2 animals). They varied between 0 and 3% and at first we thought it possible that no straining took place at all and that the values found might be due to variations in the colorimeter readings. This, however, was not the case.

11. *Colloids*

As has been shown above, even very small particles, like those of carbon black, are partly retained. We may therefore suppose that also colloid particles will be kept back, but if the extent of straining is proportional to the diameter of the particles, it will be so low as to escape observation. Fox, Sverdrup, and Cunningham (1937) believed they had established with certainty that colloids are retained completely during one single passage of the water through the gills. Fox and Coe (1943) made reference to some preliminary experiments with colloids, such as Congo red and soluble starch, which, they believed, showed that both substances were strained out. We found, however, that these substances are not suitable for experiments. Congo red is adsorbed to the tissue of the gills and therefore decreases in concentration through adsorption and not as a result of straining. Soluble starch rapidly flocculates in seawater and the large floccules are then strained out.

The fact that the colour of Congo red disappears as a result of the mussel's activity does not prove that colloids can actually be retained in another way than through adsorption, for proper solutions will decrease in concentration in the same way. Korringa (1952) observed that fountain pen ink was removed by mussels in a short time. The same holds for methylen blue. It stains the gills and the mantle edge a blue colour, but the mucus in the food groove is coloured only a very light shade of blue. In one of our own experiments a mussel was kept in a solution of ± 1 mg per l of the yellow dye dipicrylamine, which is strongly adsorbed to organic material. The concentration in a vessel containing one litre decreased as follows:

at the start	1.09
after one hour	0.87
after two hours	0.78

The concentration of the control solution in a similar vessel without a mussel fell in two hours to 1.02 mg/l.

The yellow colour was strongly adsorbed to mantle and gills.

These results seem to show that the straining percentage of colloids is negligible. Adsorption, e.g. of dyes, and perhaps of ions, will indeed take place, but this is not straining, and only if adsorption to mucus takes place, some of these substances may be taken up with the food.

Summarizing the results of the above observations on straining, we find the following.

Mussels retain spores of *Lycopodium*, with a size of 30–40 μ, to the extent of 93–100 %; at least 85 % of the grains of wheat starch (2–37 μ), and up to 100 % of the grains of maize starch (2–35 μ) are strained out. With starch grains only few experiments were made, but as regards *Lycopodium* spores the assumption that low straining percentages do not occur is probably warranted. These three represent the group of large particles, which are let through with difficulty.

Blood corpuscles (7–8 μ) are retained to an extent varying from 0 to 98 %. They represent the group of median particles, which may be completely retained and let through entirely. Among this group we may apparently also class an alga like *Chlorella* (5 μ), whose percentage retention, according to LOOSANOFF and ENGLE (1947), varies from 0 to 92 in *Ostrea virginica*.

Finally there is a group of small particles, which *Mytilus* strains out to an extent that falls a good deal short of 100 %. It is represented by milk particles (about 0.14–6.3 μ), strained out in our experiments to an extent varying from 0 to 60 %; flagellates (about 1.5–2.5 μ), of which 0-50 % were retained; bacteria (about 0.5–2.5 μ), percentage retention 0–24; and finally carbon black and colloids, which are hardly retained at all.

It appears that, for small particles, the maximum values observed for the straining are more or less proportional to the diameter of the particles and not to their surface.

B. STRAINING OF MIXTURES

The foregoing results suggest that there is a definite connection between straining and particle size. To investigate this connection more closely a number of mixtures of two suspensions of different particle size were made and fed to mussels. If indeed we had to do with a matter of particle size the straining percentage for such mixtures would correspond with the value found for the average of the particle sizes of the two components. The suspensions were diluted to such an extent that both had the same extinction value in the colorimeter; then, equal parts were mixed. The results are given in table VII.

TABLE VII
Straining of mixtures.

	Straining percentage separate suspensions	Straining percentage mixtures (calculated)	Straining percentage mixtures (observed)	Numbers of observations and (between brackets) those of animals
1. Carbon black *Lycopodium*	0– 3 93–100	47–52	48–51	16 (2)
2. Carbon black Silt 12 μ	0– 3 58–100	29–52	38–52	15 (2)
3. Carbon black Blood	0– 3 0–98	0–51	18–40	15 (2)
4. Blood *Lycopodium*	0– 98 93–100	47–99	50–68	19 (2)
5. Blood Silt 12 μ	0– 98 58–100	29–99	75–97	41 (2)
6. Silt 12 μ *Lycopodium*	58–100 93–100	76–100	78–100	14 (3)

Table VII suggests that a mixture of two suspensions is strained as if each of the components were separate. The comparison between calculated and observed values is in agreement with this assumption. The table shows that all straining percentages actually observed are within the calculated ranges.

C. STRAINING OF SILT

Under natural conditions mussels will take in large quantities of silt. This consists of fine sand, clay, shell material, living and dead organisms and fragments of the latter. Silt of estuarine or shallow coastal water contains many coarse particles as a result of flocculation. These floccules, which can partly be seen with the naked eye, form the greater part of the silt. Vigorous shaking reduces their size.

It may be expected from the above observations that straining and especially variations in the extent of straining of silt suspensions will depend on the size distribution of the particles, and it will therefore make much difference what kind of silt suspension is used, and how long the silt has had time to settle. When e.g. a suspension has been left undisturbed for a couple of days, it will contain only particles of the small and medium size groups, and the results of straining will differ from those obtained with the original suspension.

In order to get a rough measure for the correlation between settling time and particle size, a suspension was made of 100 cc of fresh silt from the Waddensea in 10 litres of seawater. It was thoroughly stirred and then given time to settle. Beforehand shell or other coarse material had been strained off through a 1 mm sieve. From time to time a sample of this suspension was taken by means of a wide mouth sampling pipette at a depth of 10 cm. The maximum diameter of the particles of the sample was approximately measured under the microscope,

TABLE VIII

Particle size of settling silt.

Time after start (in minutes)	Maximum diam. of particles in μ (approx.)	Colorimeter extinction in violet light (4200Å) (partly extrapolated)	Colorimeter extinction in red light (7000Å) (partly extrapolated)	Relation between extinctions in violet and red light	Dry weight of silt in 100 cc of water (in mg)	% of silt removed by settling
0	300	4.500	3.100	1.46	333.8	0
5	200	1.800	1.180	1.52	54.4	83.8
15	120	0.670	0.430	1.56	25.5	92.3
30	50	0.610	0.375	1.62	14.8	95.4
60	40	0.450	0.245	1.82	11.9	96.4
120	30	0.200	0.095	2.10	4.3	98.7
240	25	0.185	0.080	2.30		
480	20	0.130	0.045	2.90		

colorimeter extinction readings were made, and the dry weight of the silt present in 100 cc of water was also determined. In this way the data of table VIII were obtained.

It seems obvious that, though smaller particles occur, the greater part of the silt consists of large particles, of a size that mussels, according to our above observations, must be able to strain out easily.

Two samples of this silt were used to determine the percentage of straining by a mussel. One sample was taken after 1–2 hours' settling and its maximum particle size was 30–40 μ. It is difficult to say what may have been the average size. A second sample was taken after 16 hours' settling; the maximum size of its particles was 12 μ. The results are given in fig. 11. They relate to 5 and 8 mussels respectively.

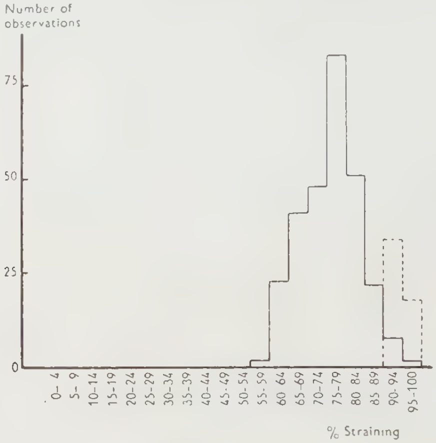

Fig. 11. Frequency distribution of straining percentages for silt suspensions. The continuous line represents values for silt with a maximum particle diameter of 12 μ (data for 8 animals added up), the dotted line values for a maximum particle size of 30–40 μ (data for 5 animals).

In the case of a sample with a maximum particle size of 30–40 μ the extent of straining was 90–99 %, the percentage retention of the sample with a maximum particle size of 12 μ was 58–100, with a peak around 80.

These results at the same time indicate that the suspensions in question contained a negligible amount of particles of small size (e.g. below 3 μ), otherwise no straining of 100 % would have been observed.

V. DIRECT OBSERVATIONS

Mr. J. W. DE BLOK, who worked at the Zoological Station in the summer of 1952, drew our attention to the fact that in young mussels

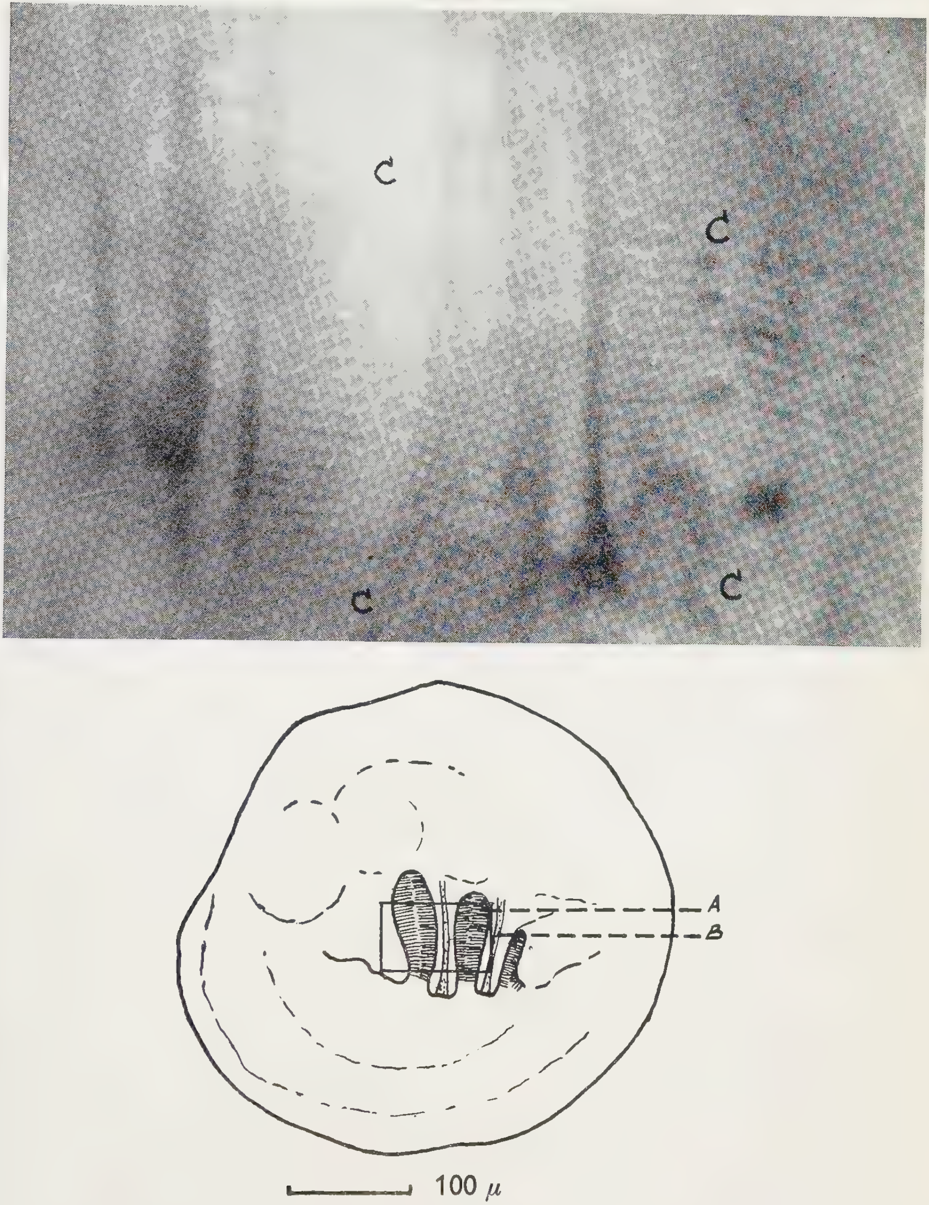

Fig. 12. Scheme of position of gills of young mussel, showing the frontal edges of two filaments (B) and the rows of latero-frontal cilia on both sides of the ostia (A). The part of the gills within the rectangle is reproduced in the microphotograph, in which two double rows of latero-frontal cilia are visible, which interlock at the ends (along the vertical line CC). In reality the photograph refers to a mussel somewhat older than that in the figure.

of about 500 μ length the ciliary activity can be seen right through the shells. In the summer months these small mussels can be found in abundance on the red alga *Ceramium*. This provided an opportunity for direct observations on the straining process. Our observations were made under 360 × magnification on mussels placed in a hanging drop of a carmine suspension in a moist chamber. Only a few gill filaments are to be observed in such young animals and the number of ostia is mostly 2–4 (fig. 12).

It was observed that the carmine particles may stick for a moment to the long latero-frontal cilia. When a particle adheres to a cilium, the latter decreases its rate of beating and then the particle is wiped off by a peculiar movement on to the row of frontal cilia. It sometimes took two or three strokes before a particle was wiped off and a few times the particle was seen to be freed again. After we had made these observations we found that WALLENGREN (1905) described exactly the same fact.

The movement of the cilia was interrupted by periods of rest, though we could not observe whether this had anything to do with the opening or closing of the shells. At rest, the long latero-frontal cilia form a row on either side of the ostia, stretching across; this can be seen in fig. 12, which was taken through the shells. In the depth of the ostium then a faint movement of the lateral cilia is visible, but no water current comes from the exhalent aperture. The pumping begins again like an explosion, the cilia all together start a vigorous beating and at the same time a jet of water can be seen from the exhalent aperture.

It was also observed that large particles are held back by the mantle edge. The edges then transport these large particles to the place where the pseudofaeces are discarded. The mantle, which has a fringed edge like old lace, thus preselects the larger particles. The transport of material and the formation of pseudofaeces by the ciliar streams of the mantle cavity were, however, not further studied by us. Clogging of particles in the slits of the ostia was not observed.

The mechanism, as we observed it in young mussels, is not that of a sieve with meshes; it rather consists in the catching of particles which adhere to the beating cilia.

VI. SUMMARY

1. This paper deals with the question what percentage mussels retain from the suspended material they pump through their gills, and what influence the particle size of the suspended material has on the percentage retained.

2. There is apparently no direct relation between the rate of pumping of the mussel and its efficiency in straining. The extent of straining may show greatly varying values even when pumping is constant, the percentage of material retained may be the same at different rates of pumping.

3. The percentage of particles that is retained depends on their size. Accordingly, one can divide the particles into different size groups.

A. A group of large particles which are not let through or let through with difficulty, because they are about the size of the diameter of the ostia (30–40 μ) or larger.

B. A group of median particles which may be completely retained or let through at will. Blood corpuscles of about 7–8 μ are a typical representative of this group.

C. A group of small particles, which *Mytilus* cannot completely retain in a single passage of the water through the gills. To this group belong milk particles, flagellates of 1.5–2.5 μ, and bacteria.

D. A group of particles that can hardly be retained at all. It is represented by suspensions of such substances as colloids and carbon black.

4. It appears that it is especially the diameter of the particles that is important.

5. Mixed suspensions are strained as if each of the components were separate.

6. In suspensions with particles of varying sizes the larger particles have a better chance of being caught than the smaller ones. Suspensions that have passed the gills of a mussel may therefore contain a higher percentage of small-sized particles. This was demonstrated for particles of medium size (grains of wheat and maize starch) as well as for small particles (milk). In the latter case measurements were made by an optical method, which is based on the different "extinction" values in red and violet light.

7. Silt, as a suspension of particles that vary a good deal in size, is subject to the laws stated under 5. and 6.

8. Direct microscopical observations on very young mussels suggest that suspended particles are caught by adhesion to the long laterofrontal cilia. They are then wiped off on to the frontal cilia. Similar observations had already been made by WALLENGREN (1905).

9. Our observations tend to show that MACGINITIE's view that feeding is based on filtration through a mucus layer is open to criticism and that suspended material is actually retained by a mechanism based on adhesion to sticky cilia which might be compared to moving lime twigs.

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L'ANATOMIE DE CERBERUS RHYNCHOPS

par

R.A.M. BERGMAN

(Institut Royal des Regions Tropicales, Amsterdam)

MATÉRIEL ET MÉTHODE

Le *Cerberus rhynchops* est un serpent qui se trouve à Java surtout à la côte, dans les embouchures des grands fleuves, mais aussi dans les petits cours d'eau et dans les étangs où se fait l'élevage des poissons. Tout comme l'*Homalopsis* il est redouté pour la perte qu'il occasionne parmi les jeunes poissons.

Notre matériel consiste en 78 animaux mâles et 107 femelles. La plus grande partie a été collectionnée de 1932 à 1941 à Surabaia (à l'est de Java) et le long de la côte du nord. Les mesures du corps et de la queue de 8 mâles et de 8 femelles proviennent des données de Kopstein (1931).

Comme nous l'avons décrit auparavant, les animaux furent tués par la piqûre occipitale, pesés et fixés par la transfusion dans l'aorte, d'abord de l'eau salée à 1,1 % pendant une vingtaine de secondes et ensuite du liquide de Bouin. Après quelques jours de séjour dans le formol à 10 % la paroi ventrale fut ouverte et la distance du commencement et de la fin des organes prise à partir du museau. Pour l'analyse statistique les méthodes décrites dans le manuel de Simpson et Roe (1939) ont été suivies.

Il n'y a que peu de notes sur la biologie de ce serpent: Werner mentionne qu'il est vivipare et que dans un cas donné la jetée contenait 12 petits, de 15 à 17 cm de long. Smith (1943) remarque que les "jetées" comptent de 8 à 26 animaux, qui mesurent de 175 à 200 mm. Kopstein (1931) a expérimenté avec le poison qui est effectif pour les crabes et semble donner des résultats inconstants pour le rat et les poissons. Pour l'homme il est inoffensif. Selon Smith l'animal est de nature peu agressive ce qui est exactement ce que nous avons observé à Java. Sa course sur terrain sec est assez curieuse, de la même façon que celle de l'*Homalopsis* (1951). Les animaux lèvent d'abord le tiers d'avant du corps, retirent la tête un instant et puis semblent la projeter en avant avec quelque force de sorte que le reste du corps semble entraîné plus ou moins en ligne droite. Il est parfois difficile de voir quelle partie du corps reste en contact avec le sol.

Dans la série quelques animaux avaient des restes de proie dans l'estomac, une femelle longue de 482 mm (museau–cloaque) et une autre de 771 mm, un mâle de 557 mm avait des restes dans l'oesophage.

Une femelle de 505 mm a été injectée avec la fuchsine acide à 1 $^0/_{00}$ dans l'eau salée; après découpage les deux tiers craniaux de l'estomac étaient jaunes, le tiers caudal rouge. Les essais de nutritions n'avaient que peu de succès: des animaux qui reçurent de la purée de poisson il n'y a que quelques uns qui ont vécu plus de deux jours après l'alimentation forcée. Inutile de dire que cette alimentation a été faite avec patience et prudemment, de façon à ne pas injurier les muqueuses.

Une femelle de 624 mm a été injectée au venin de cobra et fut trouvée morte le lendemain; un mâle de 438 mm a été mordu par une *Lapemis hardwickei* et se trouva 24 heures après en parfaite condition.

Comme pathologie nous avons trouvé un cas (un mâle de 554 mm) où la paroi de l'estomac était soudée à la paroi ventrale formant un canal qui aboutissait sous la peau à une petite tumeur inflammatoire.

Les données sur l'analysis des sels du plasma sanguin ont été perdues par suite de l'occupation japonaise.

TABLE I

Mesures maxima

	Sexe inconnu			Mâles			Femelles		
	corps	queue	total	corps	queue	total	corps	queue	total
DE ROOY 1916	800	180	980						
TAYLOR 1921				815	152	967	960	170	1130
SMITH 1943				770	115	885	1000	180	1180
BERGMAN				695	180	875	820	169	989

CROISSANCE

Quant aux nouveau-nés nous avons les données de WERNER dans BREHM qui les dit de 15 à 17 cm de long, et SMITH (1943) qui donne 175 à 200 mm. Nos plus petits spécimens, une femelle de 291 mm et un mâle de 330 mm ne portaient déjà plus la cicatrice ombilicale, tous deux furent pris en août.

La répartition des longueurs des animaux pris dans les différents mois des années 1932 à 1941 est cependant irrégulière (fig. 1). Tout d'abord il nous manque les nouveau-nés, qui se trouvent parfaitement bien dans d'autres séries de nos serpents. Ensuite il y a un vide pratiquement de septembre à janvier sans que cela puisse s'expliquer (comme celui de novembre) par l'interruption du travail au laboratoire. Il me semble aussi que dans les séries rangées par mois il y a un certain groupement, mais malheureusement les données sont trop incomplètes pour en permettre l'emploi pour une analyse du phénomène de la croissance.

FERTILITÉ

En ce qui concerne l'évolution embryonnaire nous avons les données suivantes: les œufs se trouvent d'abord dans les ovaires comme des rangées régulières de petits points blanc-jaune, gros comme une tête d'épingle. Ensuite ils grossissent et forment de petites sphères régulières jusqu'à 3 mm de diamètre. Dès lors la croissance se fait surtout dans le sens de la longueur, les œufs deviennent ovaux, ce qui se voit très

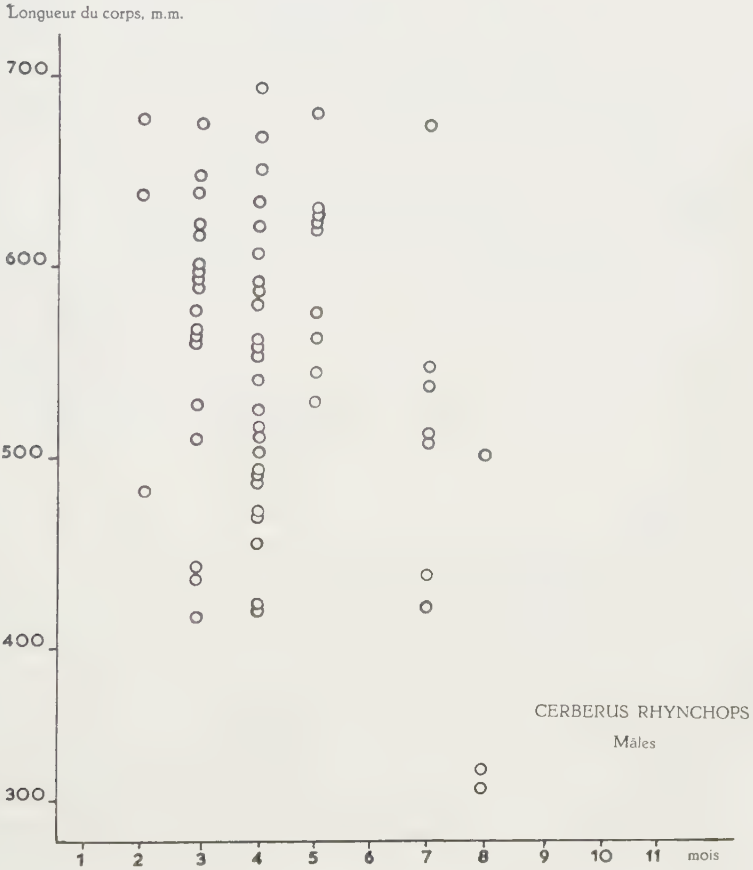

Fig. 1. La répartition des *Cerberus rhynchops* mâles, placés par ordre de la longueur du corps dans les différents mois de l'année.

facilement dès que le diamètre long atteint 5 ou 6 mm. Les œufs sont transférés de l'ovaire dans le tube utérin quand ils ont environ 20 mm de long. A ce moment on n'y voit pas encore à l'œil nu des embryons: leur futur développement se fait dans l'utérus.

Dans notre série la plus courte femelle portant des œufs de 6 mm mesure 572 mm. Dans la courbe de Galton (fig. 2) nous trouvons le premier coude un peu au delà de 500 mm ce qui est une longueur notablement inférieure.

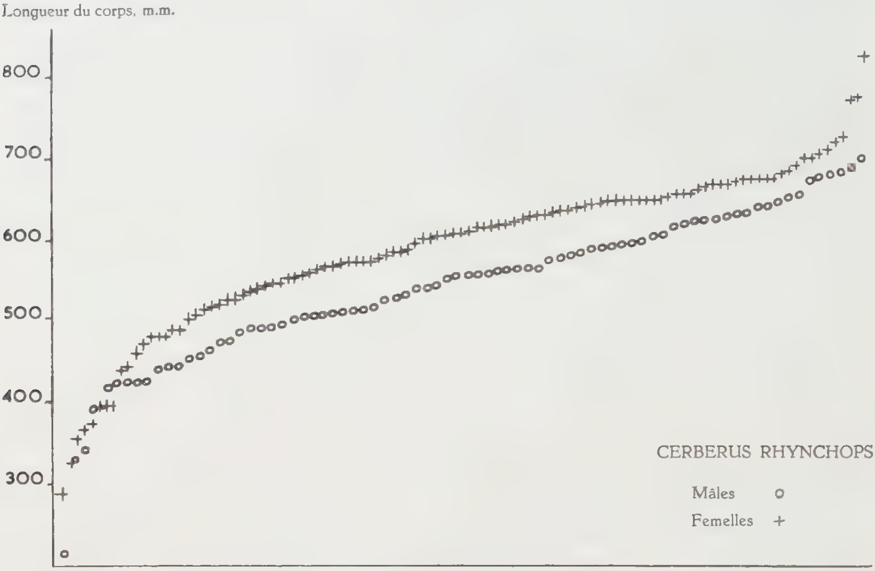

Fig. 2. Les animaux placés par ordre de la longueur du corps.

Nous trouvons noté que dans une femelle de 672 mm de long, prise en avril, les œufs qui se trouvaient dans l'utérus étaient jeunes et il y avait des corps jaunes dans les ovaires. Dans une femelle de 653 mm, l'intestin se trouvait en position ventrale de l'utérus qui contenait les œufs.

D'autre part nous trouvons des œufs dans l'utérus de femelles capturées en mars, avril, mai, juillet et octobre, ce qui est en somme la plus grande partie de l'année. Comme par suite de la guerre le matériel a disparu, il n'est plus possible d'examiner s'il y avait une croissance marquée des embryons pendant ces mois ni de vérifier l'hypothèse d'une ovulation régulière en mars–avril, avec la jetée vers la fin de l'année.

Le nombre d'œufs est noté dans la table II:

TABLE II

Longueur du corps	Oeufs à droite	gauche	Total
573	8	7	15
653	9	—	9
672	9	5	14
678	10	6	16
681	9	8	17
771	14	9	23
820	24	11	35

Ce qui indique très probablement que le nombre d'œufs augmente avec l'âge.

DONNÉES TOPOGRAPHIQUES

En prenant, dans le cas présent un peu arbitrairement, tous les animaux au delà du premier coude de la courbe galtonienne comme adultes, nous trouvons une longueur du corps plus courte chez les mâles: 567,2 mm que chez les femelles: 610,4 mm. Ici D σD = 4,0 indiquant une différence nettement significative. Nous voyons d'ailleurs que les courbes galtoniennes pour les deux sexes donnent une illustration de ce fait: les lignes pour la période adulte sont à peu près parallèles, celle pour les mâles se trouve en dessous de celle des femelles.

Pour la queue nous voyons aussi une différence sexuelle significative D/σD =6,4. Seulement la direction de cette différence est de sens inverse à celle de la différence entre les longueurs du corps: les mâles au corps plus court ont la queue plus longue.

La différence de longueur du corps entre les deux sexes entraîne une pareille différence pour chacune des données topographiques en valeur

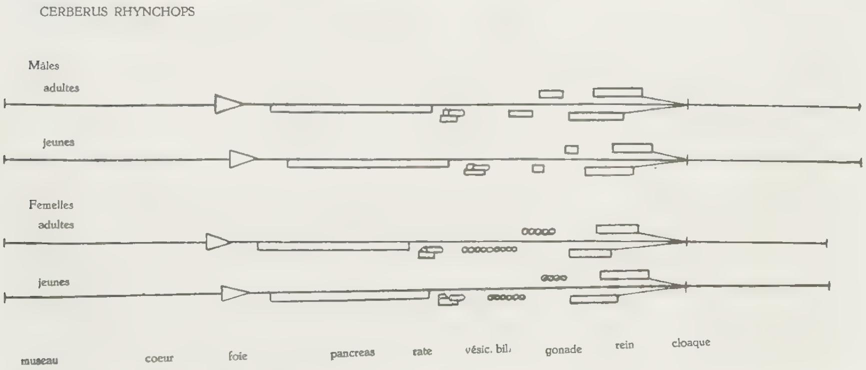

Fig. 3. Les données topographiques de *Cerberus rhynchops* en promille de la longueur du corps.

absolue. Pour effectuer une comparaison utile, il faut recourir à la projection de ces données en $^0/_{00}$ de la longueur du corps (fig. 3 et table III). On voit alors que chez les mâles la queue mesure 252 $^0/_{00}$ du corps, chez la femelle 208 $^0/_{00}$.

Toutes les mesures concernant les organes de la moitié craniale du corps ont des valeurs plus élevées chez les mâles (table IV et V), ce qui signifie que ces organes ne s'étendent chez les femelles que jusqu'a 640 $^0/_{00}$ du corps et chez les mâles jusqu'a 671 $^0/_{00}$. Au contraire les reins se trouvent chez les deux sexes à la même place. La différence

TABLE III

Topographie des organes en $^0/_{00}$ de la longueur du corps.

		Mâles		Femelles	
		jeunes	adultes	jeunes	adultes
Longueur corps M		391	567	371	610
	$^0/_{00}$	1000	1000	1000	1000
	queue	255	252	209	208
Coeur	Lim. cran.	328	308	315	294
	lim. caud.	365	346	354	328
	longueur	38	36	39	36
Foie	lim. cran.	411	388	385	368
	lim. caud	650	623	620	590
	longueur	238	233	240	226
Vés. bil.	lim. cran.	685	650	648	615
	lim. caud.	708	671	670	640
	longueur	23	23	24	23
Pancréas	lim. cran.	672	638	632	603
	lim. caud	700	660	660	627
	longueur	28	23	28	24
Rate	lim. cran.	676	640	632	608
	lim. caud.	689	648	641	616
	longueur	12	9	9	8
Gonades dr.	lim. cran.	775	734	706	666
	lim. caud.	793	771	765	750
	longueur	18	38	59	81
Gonades g.	lim. cran.	820	781	786	755
	lim. caud.	838	815	822	805
	longueur	18	35	36	51
Longueur des deux		36	75	95	130
Rein dr.	lim. cran.	850	825	825	824
	lim. caud.	920	904	895	891
	longueur	71	78	65	67
Rein g.	lim. cran.	889	860	870	866
	lim. caud.	950	931	940	930
	longueur	67	74	67	64
Longueur des deux		138	153	136	135

entre les distances des organes craniaux aux reins n'est pas très grande, mais il est facile de voir qu'elle va de pair avec le développement des gonades qui nécessite un espace plus considérable chez la femelle que chez le mâle.

De même pour les longueurs des organes les valeurs absolues sont moins importantes que les dimensions relatives: et dans ces dernières nous trouvons une concordance complète chez les deux sexes, sauf évidemment pour les gonades et pour les reins (table VI); les testicules sont comme de règle beaucoup plus courts que les ovaires. En outre il semble que les reins soient plus courts chez les femelles: 67 et $64\,^0/_{00}$ tandis que chez les mâles ils comptent 78 et $74\,^0/_{00}$ de la longueur du corps.

Au point de vue de la symmétrie bilatérale, les gonades et les reins sont chez le mâle de même dimension à droite et à gauche: $D/\sigma D = 1{,}7$ et 1,5. Chez les femelles les reins des deux côtés ne diffèrent pas beaucoup: $D/\sigma D = 1{,}8$ mais l'ovaire droit est beaucoup plus long que celui de gauche: $D/\sigma D = 9{,}4$.

TABLE IV

Topographie, mâles adultes.

	N	R	$M \pm \sigma m$	$\sigma \pm \sigma\sigma$	$v \pm \sigma v$	σm^2
Longueur de						
Corps	65	452–695	567,2 ± 7,8	63,0 ± 5,5	11,1 ± 1,0	61,0
Queu	65	112–180	142,8 ± 2,1	16,5 ± 1,5	11,6 ± 1,0	4,2
Sommet de						
Cœur	57	142–211	175,4 ± 2,4	18,1 ± 1,7	10,4 ± 1,0	5,8
Foie	57	175–274	219,7 ± 3,0	22,9 ± 2,1	10,4 ± 1,0	9,2
Vés. bil. . . .	57	296–457	369,2 ± 5,5	41,0 ± 3,8	11,1 ± 1,0	29,7
Pancréas . .	57	297–459	362,3 ± 5,3	40,2 ± 3,8	11,1 ± 1,0	28,4
Rate	57	300–457	363,2 ± 5,3	40,0 ± 3,7	11,0 ± 1,0	28,1
Test. dr. . . .	57	343–518	415,7 ± 6,0	45,2 ± 4,2	10,8 ± 1,0	36,0
Test. g. . . .	57	362–543	442,9 ± 6,2	46,6 ± 4,3	10,4 ± 1,0	38,2
Rein dr. . . .	57	367–563	467,0 ± 6,9	51,9 ± 4,9	11,1 ± 1,0	47,4
Rein g. . . .	57	383–591	488,1 ± 7,2	54,6 ± 5,1	11,2 ± 1,0	52,6
Fin de						
Cœur	57	159–239	196,5 ± 2,7	20,2 ± 1,9	10,3 ± 1,0	7,15
Foie	57	287–440	352,8 ± 5,0	37,8 ± 3,5	10,7 ± 1,0	25,1
Vés. bil. . . .	57	303–476	381,3 ± 6,1	46,2 ± 4,3	12,1 ± 1,1	37,6
Pancréas . .	57	308–475	375,0 ± 5,5	41,6 ± 3,8	11,1 ± 1,0	30,5
Rate	57	305–463	367,9 ± 5,3	40,8 ± 3,8	11,1 ± 1,0	28.1
Test. dr. . . .	57	358–545	436,6 ± 6,4	48,6 ± 4,5	11,1 ± 1,0	41,1
Test. g. . . .	57	372–568	463,3 ± 6,9	52,1 ± 4,9	11,1 ± 1,1	47,7
Rein dr. . . .	57	404–621	513,1 ± 7,3	55,6 ± 5,2	10,8 ± 1,0	53,6
Rein g. . . .	57	413–645	528,8 ± 8,1	61,5 ± 5,8	11,6 ± 1,1	66,5

VARIABILITÉ

Pour les données topographiques les coefficients de variation vont de 10,3 à 11,6 chez les mâles et de 10,7 à 12,1 chez les femelles.

Pour les longueurs des organes il y a un rangée de 13,2 à 25,2 chez les mâles et de 11,5 à 22,7 chez les femelles si l'on ne compte pas les ovaires. Pour ces derniers la variabilité à droite semble moins grande qu'à gauche, mais $D/\sigma D = 1,8$ trop petit pour être significatif. Peut-être y a-t-il dans les valeurs de ces coefficients un certain groupement: cœur et foie 14,8 et 13,2 chez les mâles, 16,5 et 11,5 chez les femelles; pancréas et reins à droite et à gauche 17,1 – 18,7 – 18,4 chez les mâles, et 15,1 – 21,2 – 17,8 chez les femelles. Enfin les petits organes: vésicule biliaire et la rate et les gonades 23,0 – 24,0 – 25,2 – 23,9 chez les mâles et 22,7 – 24,6 – 28,5 – 34,6 chez les femelles.

INTERVALLES

Les intervalles (tables VII et VIII) entre les organes offrent certaines particularités: pour la distance du foie à la vésicule biliaire, la varia-

TABLE V

Topographie, femelles adultes.

	N	R	$M \pm \sigma m$	$\sigma \pm \sigma\sigma$	$\sigma \pm \sigma v$	σm^2
Longueur de						
Corps	97	461–820	610,4 ± 7,3	72,2 ± 5,2	11,8 ± 0,8	53,6
Queu	95	97–169	126,9 ± 1,4	13,7 ± 1,0	10,8 ± 0,8	2,0
Sommet de						
Cœur	84	137–238	179,5 ± 2,2	19,8 ± 1,5	11,0 ± 0,8	4,7
Foie	84	171–302	224,3 ± 2,7	25,1 ± 1,9	11,2 ± 0,9	7,5
Vés. bil. . . .	84	278–463	375,8 ± 4,5	41,0 ± 3,2	10,9 ± 0,8	20,0
Pancréas . .	84	273–455	368,0 ± 4,4	40,7 ± 3,1	11,4 ± 0,9	19,7
Rate	84	275–458	370,8 ± 4,4	40,7 ± 3,1	11,0 ± 0,8	19,7
Ovaire dr. . .	84	305–501	407,3 ± 4,9	45,2 ± 3,5	11,1 ± 0,9	24,9
Ovaire g. . .	84	348–585	460,9 ± 4,5	49,2 ± 3,8	10,7 ± 0,8	28,8
Rein dr. . . .	84	373–641	502,6 ± 6,4	58,9 ± 4,5	11,7 ± 0,9	41,3
Rein g. . . .	84	394–690	529,3 ± 6,9	63,4 ± 4,9	11,9 ± 0,9	47,8
Fin de						
Cœur	84	153–269	200,3 ± 2,5	23,1 ± 1,8	11,5 ± 0,9	6,5
Foie	84	280–467	360,2 ± 4,3	38,8 ± 3,0	10,8 ± 0,8	18,1
Vés. bil. . . .	84	286–485	390,5 ± 4,7	42,6 ± 3,3	10,9 ± 0,8	21,6
Pancréas . .	84	285–473	383,0 ± 4,7	42,9 ± 3,3	11,2 ± 0,9	22,9
Rate	84	280–465	376,0 ± 4,4	40,7 ± 3,1	10,8 ± 0,8	19,7
Ovaire dr. . .	84	336–585	458,0 ± 5,7	52,5 ± 4,0	11,5 ± 0,9	32,8
Ovaire g. . .	84	366–628	491,2 ± 6,2	56,5 ± 4,4	11,5 ± 0,9	38,2
Rein dr. . . .	84	402–707	544,2 ± 7,2	65,7 ± 5,1	12,1 ± 0,9	51,5
Rein g. . . .	84	420–753	567,9 ± 7,5	69,0 ± 5,3	12,1 ± 0,9	56,7

bilité est beaucoup plus grande chez les mâles, V =55 que chez les femelles où V =10,5. Pour toutes les autres distances les deux sexes présentent des valeurs proches l'une de l'autre. En général la variabilité de ces mesures n'est pas très grande chez *Cerberus rhynchops*.

CORRÉLATIONS

La corrélation (table IX) entre la longueur du corps et le poids est plus haute chez les mâles que chez les femelles: le facteur z montre dans ces deux cas une différence de 1,60 à 1,06 et D/σD =3,5. Dans la fig. 4 la différence n'est pas claire.

Pour la longueur du corps et celle de la queue la corrélation est

TABLE VI

Longueurs des organes.

MÂLES

	N	R	M ± σm	σ ± σσ	V ± σv	σm^2
Corps	65	452–695	567,2 ± 7,8	63,0 ± 5,5	11,1 ± 1,0	61,0
Queue	65	112–180	142,8 ± 2,1	16,5 ± 1,5	11,6 ± 1,0	4,2
Coeur	57	14–29	20,4 ± 0,4	3,0 ± 0,3	14,8 ± 1,4	0,16
Foie.	57	107–171	132,1 ± 2,3	17,4 ± 1,6	13,2 ± 1,2	5,31
Vés. bil.	57	8–20	12,6 ± 0,4	2,9 ± 0,3	23,0 ± 2,2	0,14
Pancréas	57	8–18	13,6 ± 0,3	2,5 ± 0,2	18,4 ± 1,7	0,10
Rate	57	3–8	5,0 ± 0,2	1,2 ± 0,1	24,0 ± 2,4	0,03
Testic. dr.	57	8–32	22,2 ± 0,7	5,6 ± 0,5	25,2 ± 2,4	0,55
Testic. g.	57	6–32	20,5 ± 0,6	4,9 ± 0,5	23,9 ± 2,2	0,40
Testic. dr.–g.	57	15–64	42,8 ± 1,4	10,2 ± 0,9	23,8 ± 2,2	1,83
Rein dr.	57	20–66	44,0 ± 1,0	7,5 ± 0,7	17,1 ± 1,6	0,98
Rein g.	57	26–60	41,8 ± 1,0	7,8 ± 0,7	18,7 ± 1,8	1,07
Rein dr.–g.	57	46–216	86,2 ± 2,0	15,3 ± 1,4	17,8 ± 1,7	4,10

FEMELLES

	N	R	M ± σm	σ ± σσ	V ± σv	σm^2
Corps	97	461–820	610,4 ± 7,3	72,2 ± 5,2	11,8 ± 0,8	53,6
Queue	95	97–169	126,9 ± 1,4	13,7 ± 1,0	10,8 ± 0,8	2,0
Coeur	84	14–32	22,4 ± 0,4	3,7 ± 0,3	16,5 ± 1,3	0,16
Foie	84	104–184	138,2 ± 1,7	15,9 ± 1,3	11,5 ± 0,9	3,03
Vés. bil.	84	8–25	14,1 ± 0,3	3,2 ± 0,2	22,7 ± 1,8	0,12
Pancréas	84	11–21	15,2 ± 0,3	2,3 ± 0,2	15,1 ± 1,2	0,06
Rate	84	3–10	5,3 ± 0,1	1,3 ± 0,1	24,6 ± 1,9	0,02
Ovaires dr.	84	22–84	49,1 ± 1,5	14,0 ± 1,1	28,5 ± 2,2	2,38
Ovaires g.	84	14–61	31,0 ± 1,2	10,7 ± 0,8	34,6 ± 2,7	1,36
Ovaires dr.–g. . . .	84	33–137	81,4 ± 2,4	22,4 ± 1,7	27,5 ± 2,1	5,95
Rein dr.	84	26–69	40,9 ± 0,9	8,7 ± 0,7	21,2 ± 1,6	0,91
Rein g.	84	26–63	38,7 ± 0,7	6,9 ± 0,5	17,8 ± 1,4	0,50
Rein dr.–g.	84	55–129	80,5 ± 1,6	14,9 ± 1,1	18,5 ± 1,4	2,64

haute dans les deux sexes et pour la facteur z $D/\sigma D = 2{,}3$ la fig. 5 montre une différence de niveau.

TABLE VII

Mâles. Intervalles.

	N	R	$M \pm \sigma m$	$\sigma \pm \sigma\sigma$	$V \pm \sigma v$	σm^2
Museau–coeur	57	142–211	175,4 ± 2,4	18,1 ± 1,7	10,4 ± 1,0	5,8
Cœur–foie	57	14–38	24,3 ± 0,7	5,4 ± 0,5	22,2 ± 2,1	0,51
Foie–vés, bil.	57	−1 +47	16,2 ± 1,2	9,0 ± 0,8	55,5 ± 5,0	1,43
A.	57	173–281	215,9 ± 3,3	24,6 ± 2,3	11,4 ± 1,1	10,60
Pancréas–gonade dr.	57	21–57	38,7 ± 1,1	8,4 ± 0,8	21,7 ± 2,1	1,20
Gonade dr.–rein dr.	57	13–50	29,3 ± 1,3	9,4 ± 0,9	32,1 ± 3,0	1,56
Rein dr.–cloaque	57	47–84	62,0 ± 1,2	8,7 ± 0,8	14,0 ± 1,3	1,30
B.	57	101–168	130,4 ± 2,2	16,8 ± 1,5	12,9 ± 1,2	4,95
Pancréas–gonade g	57	48–95	66,1 ± 1,6	11,8 ± 1,1	17,9 ± 1,7	2,46
Gonade g–rein g	57	10–43	25,0 ± 1,1	8,4 ± 0,7	33,6 ± 3,1	1,25
Rein g.–cloaque.	57	30–63	44,0 ± 0,9	6,8 ± 0,6	15,5 ± 1,5	0,81
C.	57	99–179	134,3 ± 2,4	17,9 ± 1,8	13,3 ± 1,2	5,61
A + B.	57	284–434	346,3 ± 4,8	36,6 ± 3,6	10,6 ± 1,0	23,30
A + C.	57	286–438	350,4 ± 5,1	38,2 ± 3,7	10,9 ± 1,0	26,40
Pancréas–rein dr.	57	61–130	90,6 ± 2,2	16,8 ± 1,6	18,5 ± 1,7	4,96
Pancréas–rein g.	57	67–161	111,7 ± 2,7	20,3 ± 2,0	18,2 ± 1,7	7,25

TABLE VIII

Femelles. Intervalles.

	N	R	$M \pm \sigma m$	$\sigma \pm \sigma\sigma$	$V \pm \sigma v$	σm
Museau-coeur.	84	137–238	179,5 ± 2,2	19,8 ± 1,5	11,0 ± 0,8	4,7
Cœur–foie	84	10–33	22,3 ± 0,7	6,1 ± 0,5	27,3 ± 2,1	0,43
Foie–vés. bil.	84	−21 +48	12,8 ± 1,5	13,5 ± 1,0	10,5 ± 0,8	2,18
A.	84	152–282	214,7 ± 3,1	28,2 ± 2,2	13,1 ± 1,0	9,45
Pancréas–ov. dr.	84	1–56	24,8 ± 1,0	9,0 ± 0,7	36,3 ± 2,8	0,98
Ov. dr.–rein dr.	84	15–79	43,9 ± 1,6	14,6 ± 1,1	33,3 ± 2,6	2,52
Rein dr.–cloaque	84	47–113	70,7 ± 1,2	11,1 ± 0,9	15,7 ± 1,2	1,47
B.	84	84–221	137,6 ± 2,6	23,6 ± 1,8	17,1 ± 1,3	6,65
Pancréas–ov. g.	84	46–122	74,7 ± 1,6	14,7 ± 1,1	19,6 ± 1,5	2,57
Ov. g.–rein g.	84	4–85	37,3 ± 1,4	12,6 ± 1,0	33,9 ± 2,6	1,89
Rein g.–cloaque	84	34–83	47,1 ± 1,0	8,9 ± 0,7	18,9 ± 1,5	0,96
C.	84	114–259	158,3 ± 2,9	26,2 ± 2,0	16,5 ± 1,3	8,20
A + B.	84	247–471	354,2 ± 4,8	43,5 ± 3,4	12,3 ± 1,0	22,60
A + C.	84	277–509	374,2 ± 5,1	46,8 ± 3,6	12,6 ± 1,0	26,10
Pancréas–ov. dr.	84	68–200	118,2 ± 3,1	28,3 ± 2,2	23,9 ± 1,8	9,54
Pancréas–ov. g.	84	92–237	143,3 ± 3,3	30,0 ± 2,3	20,9 ± 1,6	10,70

Pour la longueur du corps et celle des gonades il n'y a pas de différence de corrélation entre les sexes; pour le rapport entre la longueur du corps et celle des reins la différence entre les coefficients de corrélation z des deux sexes est petite et comme $D/\sigma D = 0{,}9$ elle doit être considerée comme insignifiante. Comme pour les deux relations précédentes les diagrammes illustrent les différences de niveau.

POUMONS

L'ouverture du poumon accessoire était difficile à localiser, et la mesure n'a été prise que dans quelques cas. Le sommet du poumon et l'extrémité postérieure du sac pulmonaire sont faciles à définir avec exactitude, la transition des trabécules à la paroi lisse du sac est plutôt une zône de démarcation qu'une ligne et se laisse évaluer plutôt que mesurer avec certitude.

Les valeurs absolues dépendent de la longueur du corps et montrent une différence sexuelle, mais exprimées en $^0/_{00}$ de la longueur du corps les valeurs sont pratiquement identiques pour les deux sexes. Le sommet chez les mâles à 133 $^0/_{00}$, chez les femelles à 132 $^0/_{00}$ de la longueur du corps, la fin à 587 $^0/_{00}$ chez les mâles et 570 $^0/_{00}$ chez les femelles, la zône trabéculaire à 328 $^0/_{00}$ chez les mâles et à 316 $^0/_{00}$ chez les femelles.

TABLE IX

Mâles. Corrélations.

	N	R	M ± σm	σ ± σσ	V ± σv	r	z
Corps	67	330–695	554,4 ± 9,9	81,4 ± 7,0	14,7 ± 1,3	.922	1,60 ± 0,12
Poids	67	24–228	135,8 ± 6,4	52,1 ± 4,5	38,4 ± 3,3		
Corps	77	212–695	539,4 ± 10,5	92,0 ± 7,4	17,1 ± 1,4	.940	1,74 ± 0,12
Queue	77	61–180	136,7 ± 2,7	23,6 ± 1,9	17,3 ± 1,4		
Corps	66	330–695	550,7 ± 10,2	82,9 ± 7,2	15,0 ± 1,3	.730	0,93 ± 0,12
Gonades	66	8–64	38,5 ± 1,7	13,7 ± 1,2	35,8 ± 3,1		
Corps	66	330–695	550,5 ± 10,2	82,9 ± 7,2	15,0 ± 1,3	.865	1,30 ± 0,12
Reins	66	13–126	82,0 ± 2,2	18,3 ± 1,6	22,3 ± 1,9		
FEMELLES							
Corps	98	291–820	600,6 ± 8,8	87,4 ± 6,3	14,5 ± 1,0	.790	1,06 ± 0,10
Poids	98	18–503	160,6 ± 8,4	83,0 ± 5,9	51,5 ± 3,7		
Corps	107	291–820	589,0 ± 9,9	100,2 ± 7,0	17,3 ± 1,2	.882	1,38 ± 0,10
Queue	107	40–169	122,5 ± 2,0	20,4 ± 1,4	16,6 ± 1,1		
Corps	88	291–820	601,4 ± 9,3	87,1 ± 6,6	14,5 ± 1,1	.730	0,93 ± 0,11
Ovaires	88	22–137	76,5 ± 2,6	24,0 ± 1,8	31,4 ± 2,4		
Corps	89	291–820	601,4 ± 9,3	87,1 ± 6,5	14,5 ± 1,1	.825	1,15 ± 0,11
Reins	89	38–129	78,4 ± 1,7	16,3 ± 1,2	20,8 ± 1,6		

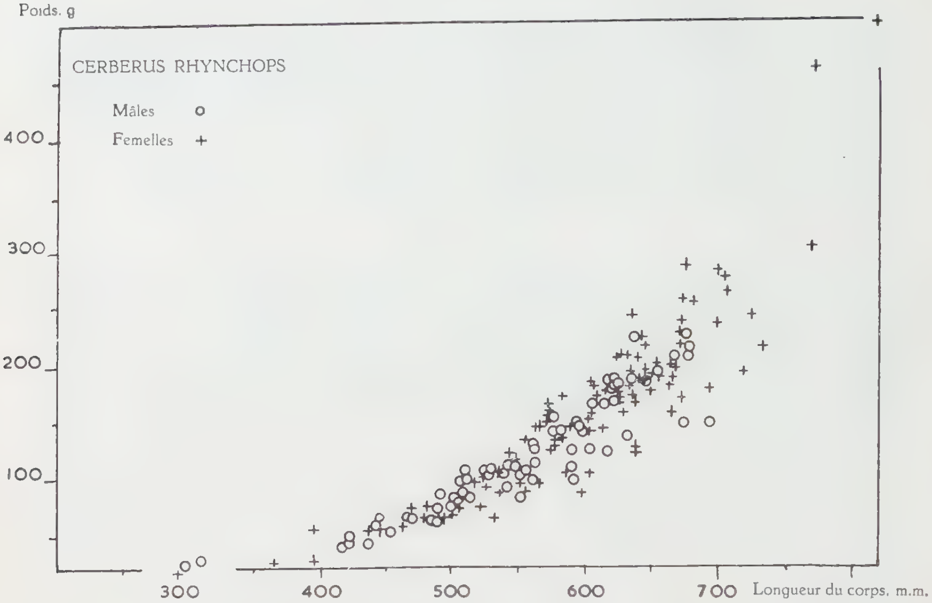

Fig. 4. La corrélation entre la longueur du corps et le poids chez *Cerberus rhynchops*.

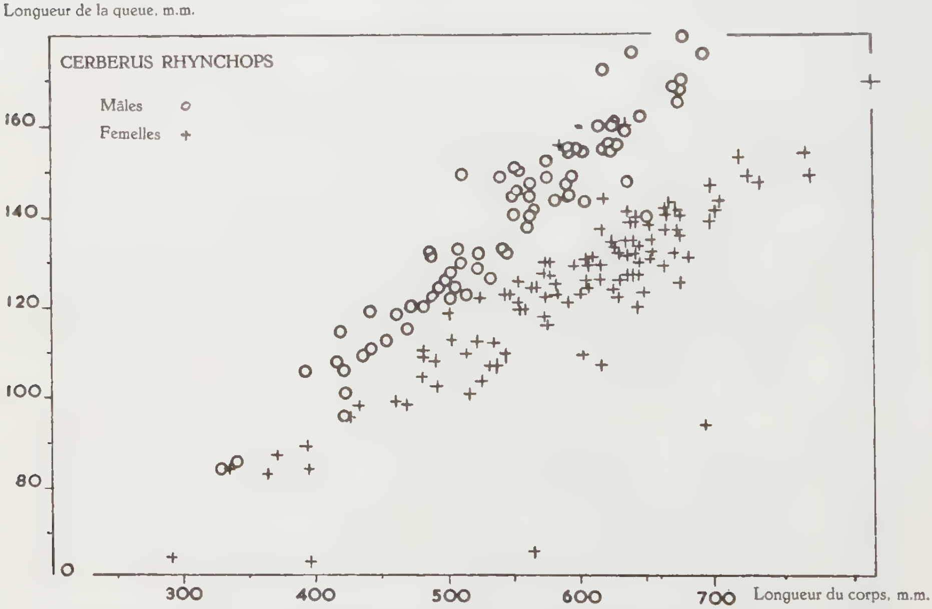

Fig. 5. La corrélation entre la longueur du corps et celle de la queue chez *Cerberus rhynchops*.

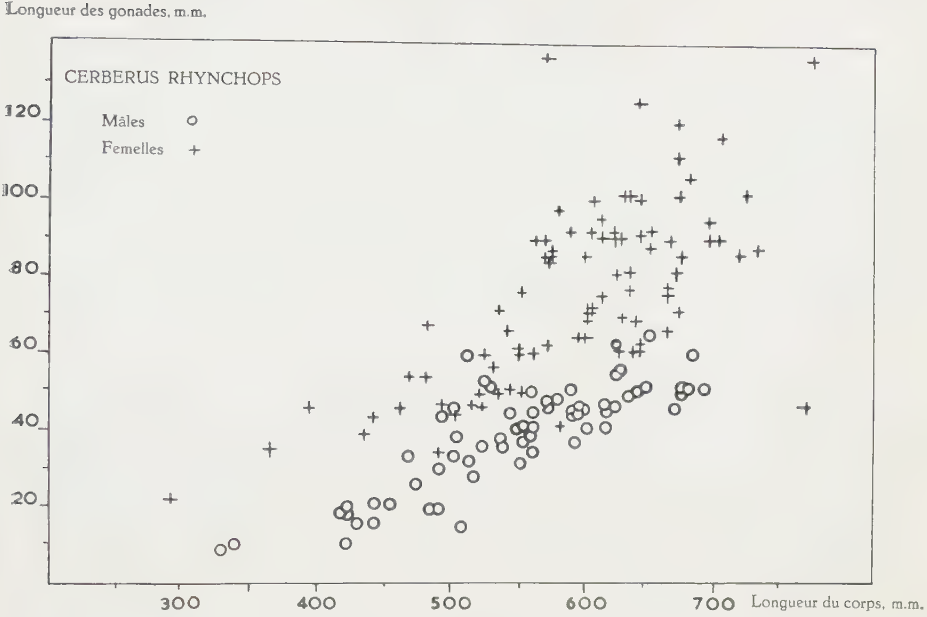

Fig. 6. La corrélation entre la longueur du corps et celle des gonades chez *Cerberus rhynchops*.

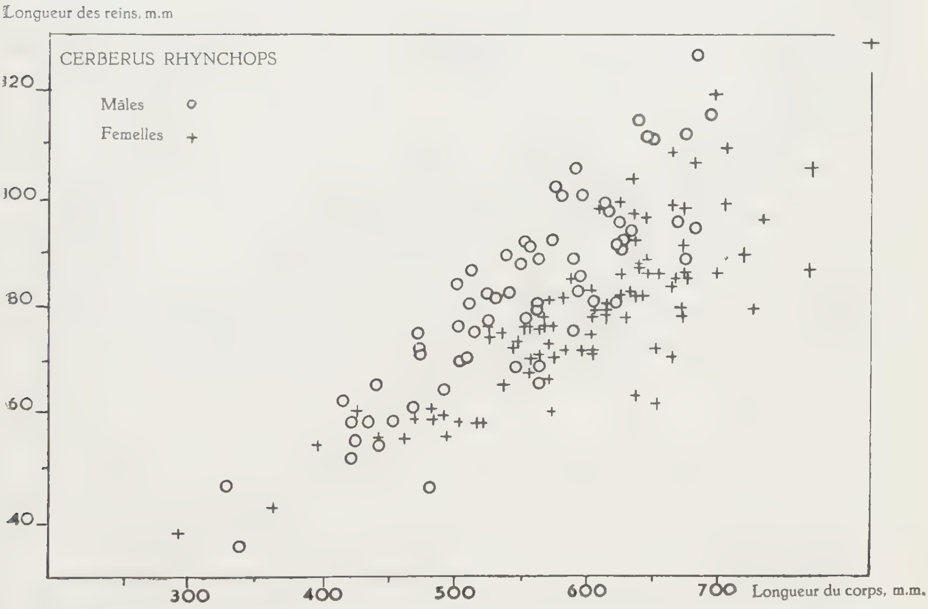

Fig. 7. La corrélation entre la longueur du corps et celle des reins chez *Cerberus rhynchops*.

TABLE X

La topographie des poumons.

Mâles sommet	57	60–97	76,4 ± 1,1	8,0 ± 0,8	10,5 ± 1,0
Femelles sommet . . .	75	60–107	80,6 ± 1,2	11,1 ± 0,9	13,7 ± 1,1
Mâles trabéc.	55	149–300	187,1 ± 3,8	28,4 ± 2,7	15,2 ± 1,4
Femelles trabéc. . . .	70	140–335	191,6 ± 3,8	32,1 ± 2,7	16,8 ± 1,4
Mâles fin	57	279–419	341,7 ± 4,9	37,0 ± 3,5	10,8 ± 1,0
Femelles fin	83	265–454	349,7 ± 4,1	37,4 ± 2,9	10,7 ± 0,8

Comme on le voit dans la table des valeurs absolues la variabilité de la mesure des zônes trabéculaires semble plus haute que pour celles du sommet ou de l'extrémité. Pour les mâles $D/\sigma D = 2{,}5$ pour les femelles $D/\sigma D = 3{,}8$, ce dernier chiffre étant significatif. La raison en est sans doute bien plus qu'une raison d'ordre biologique, la difficulté de la prise de mesure.

Amsterdam, août 1954

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L'ANATOMIE DE ENHYDRINA SCHISTOSA D

par

R. A. M. BERGMAN

(*Royal Institut des Régions Tropicales, Amsterdam*)

MATÉRIEL ET MÉTHODE

L'Enhydrina schistosa est un des serpents marins qui figure dans la collection que nous avons récoltée de 1936 à 1942 à Surabaia, à la côte Nord-Est de l'île de Java. C'est aussi un des serpents dont la morsure occasionne la mort du blessé. Pareil cas a été publié par BOKMA (1941); en 1942 nous avons publié sur ce serpent une petite note, qu'il est possible de compléter maintenant.

D'après SMITH (1926) ce serpent de mer est assez fréquent: "a common species".

D'après WALL (1921) c'est le serpent de mer le plus répandu sur les côtes de la péninsule indienne: il raconte qu'en un seul matin on lui en apporta à Cannanore dix pour chaque exemplaire d'une autre sorte; à Madras il y eut 60 *Enhydrinas* sur une collection de 192 serpents de mer. Au contraire à Colombo ils sont rares, et il n'y a que peu de notes sur l'apparition de ce serpent dans l'archipel malais.

Cependant nous n'en avons eu qu'une bonne centaine sur un total d'environ 2500 serpents marins. Nous avons demandé plusieurs fois à notre pêcheur de nous apporter plus d'exemplaires de cette espèce, sans avoir eu du succes, alors qu'il nous offrait les *Lapemis*, les *Thalassophis*, et les *Hydrophis fasciatus* en beaucoup plus grand nombre qu'il ne nous était possible d'examiner. De plus *l'Enhydrina* ne se trouvait jamais qu'en exemplaires isolés: un ou deux à la fois.

Ils se laissent reconnaître facilement, ce sont de grands serpents robustes et aplatis ayant la dimension ventrodorsale plus grande que la transversale. La couleur est d'un brun jaunâtre, foncé sur le dos, clair sur le ventre. Parfois il y a des triangles plus ou moins marqués sur les côtés. La tête est assez remarquable, aplatie et un peu en museau; la mâchoire inférieure est très mobile et s'ouvre largement.

Les animaux arrivaient vivants au laboratoire et furent déposés dans un aquarium à l'eau salée à 2,7 %, environ comme l'eau de mer. Au fur et à mesure ils étaient tués par une piqûre dans le trou occipital, pesés et fixés par transfusion par l'aorte, d'abord avec de l'eau salée à 1,1 % pendant une vingtaine de secondes, jusqu'à l'expulsion de la plus grande partie du sang et ensuite avec le liquide de Bouin pendant une heure. Ensuite ils étaient déposés dans un bassin contenant du formol à 10 %. Après quelques jours ils étaient ouverts et la position des organes était mesurée (BERGMAN 1949).

Notre matériel comprend 48 femelles et 51 mâles. Les chiffres diffèrent un peu de notre communication précédente en partie par des acquisitions ultérieures, mais encore parce qu'une partie des données fut perdue à la suite de l'occupation Japonaise; cependant dans le cas de *l'Enhydrina* la perte n'est pas grande.

PATHOLOGIE, POISON

Dans notre série il y a quelques notes sur la pathologie: à un serpent mâle de 679 mm de long (du museau à la cloaque) l'œil droit manquait, une femelle un peu plus longue, 783 mm, portait une tumeur à la mâchoire supérieure, une autre femelle de 724 mm, avait un ulcère sur la paroi extérieure du corps, dans cet animal la vésicule biliaire se trouve notée comme "Pâle". Dans un mâle de 672 mm le même organe est décrit comme portant deux tumeurs, ensemble de 14 mm de long. Une femelle de 716 mm avait les restes d'une proie dans l'estomac et une arête de poisson avait transpercé la paroi de l'estomac en sortant par la peau du ventre, sans qu'il y ait, du moins à vue d'œil, des symptomes quelque peu marqués d'inflammation. Enfin il y avait un cas d'amaigrissement marqué dans un mâle de 643 mm et trois cas de défauts de développement, une fois dans une femelle de 793 mm, où le rein gauche manquait, de même que l'utérus droit; l'utérus à gauche étant très mince, et deux fois dans deux femelles de 734 mm et de 850 mm le poumon ne montrait pas l'interruption derrière le cœur qui se trouve d'ordinaire chez ces animaux.

Plusieurs de ces cas auraient sans doute mérité une étude microscopique plus détaillée, mais comme par suite de l'occupation tout le matériel fixé est perdu, cela est malheureusement impossible.

Un des serpents, une femelle de 843 mm, a mordu un autre de 583 mm; l'unique effet visible était un ralentissement marqué du mouvement de ce dernier. Dans le cas publié par BOKMA (1941) un serpent de 33 cm de long a mordu un homme qui en est mort. Cet auteur remarque que l'on sait peu de chose sur ce poison. Ceci n'est pas étonnant: on n'obtient pas très fréquemment ce serpent à Java et il est beaucoup plus difficile d'en tirer le venin que d'obtenir celui du cobra ou de la vipère. Quand on introduit un verre de montre dans le bec de *l'En-*

hydrina, celle-ci ouvre le bec aussi largement que possible au lieu de mordre et la quantité de mucus dans la bouche est trop grande pour permettre de récolter le venin plus ou moins pur.

La manière que nous employions pour obtenir ce poison est de tenir le serpent par la tête, le dos en bas et le bec ouvert dans la main gauche. Avec la main droite on peut faire un massage de la tête ou de la mâchoire supérieure. Parfois on arrive de cette façon à vider la glande vénimeuse et on voit alors le poison sortir de la dent en une goutte claire et couler le long de celle-ci dans la gouttière formée par la muqueuse buccale. Un assistant se tenant prêt avec une seringue à fine aiguille peut aspirer le venin de cette gouttière. En somme c'est une méthode plutôt lonque et incertaine, mais je n'en connais pas de meilleure. Wall (1921) donne certaines indications au sujet de la toxicité, qui serait dix fois plus grande que celle du venin du cobra.

MESURES

Les mesures maxima que j'ai trouvées dans la litérature et celles de notre série de Surabaia se trouvent dans la table ci-dessous:

	Mâles			Femelles			Sexe inconnu		
	corps	queue	total	corps	queue	total	corps	queue	total
De Rooy (1916)							1110	190	1300
Wall (1921)			1398			1310			
Smith (1943)							1200	200	1400
Bergman	867	141	1008	938	136	1074			

Les mesures de serpents nouveau-nés sont d'après Wall (1921) 254 à 279 mm. Les plus petits animaux de Surabaia avaient une longueur totale de 378 mm pour les femelles et 453 mm pour les mâles.

SEXES, FERTILITÉ

La proportion des sexes est dans notre groupe 1 : 1 (48 : 51) quoique Wall (1921) suppose à Ceylon une proportion de 1 : 2 (5 mâles et 8 femelles, 7 embryons mâles, 12 femelles).

Dans la série de Wall (1921) la plus courte femelle enceinte mesurait 965 mm en tout. D'après cet auteur la croissance serait marquée par les dates suivantes: naissance 254–280 mm, fin de la première année 500–600 mm, fin de la deuxième année 760 mm ("from very meagre figures") maturité 965 mm, maximum 1300 mm. La naissance se trouve en février, mars, avril et mai; il y a de grands œufs en novembre et décembre; un jeune serpent de 317 mm fut pris en juin.

Dans notre série la plus courte femelle où les œufs commençaient à grandir mesurait 624 mm (corps et tête), la plus courte femelle enceinte mesurait 685 mm. Les plus petites spécimens sont pris en décembre et février, les grands œufs se montrent dans l'ovaire en juin et juillet, les œufs contenants des embryons se trouvent dans l'utérus en août et septembre, ce qui fait supposer que pour la région autour de Surabaia le commencement du développement des œufs se trouve en avril, l'ovulation en juillet et la naissance à la fin de l'année en novembre. Une femelle de 511 mm (corps et tête) porte encore dans notre liste la mention "juvénile", les dates sur les femelles portant les embryons dans l'utérus et de grands œufs dans l'ovaire se trouvent dans la table ci-dessus.

Mois	Des oeufs de plus de 20 mm dans l'ovaire				Mois	Embryons dans l'utérus			
VII	800	6	2	8	I	685	3	2	5
VIII	806	4	3	7	I	755	2	3	5
VII	835	4	3	7	VIII	762	4	7	7
VII	839	6	3	9	VIII	887	5	4	9
VI	843	2	3	5	VIII	938	4	5	9
VIII	852	3	3	6	—	—	—	—	—
VI	903	7	—	7	—	—	—	—	—

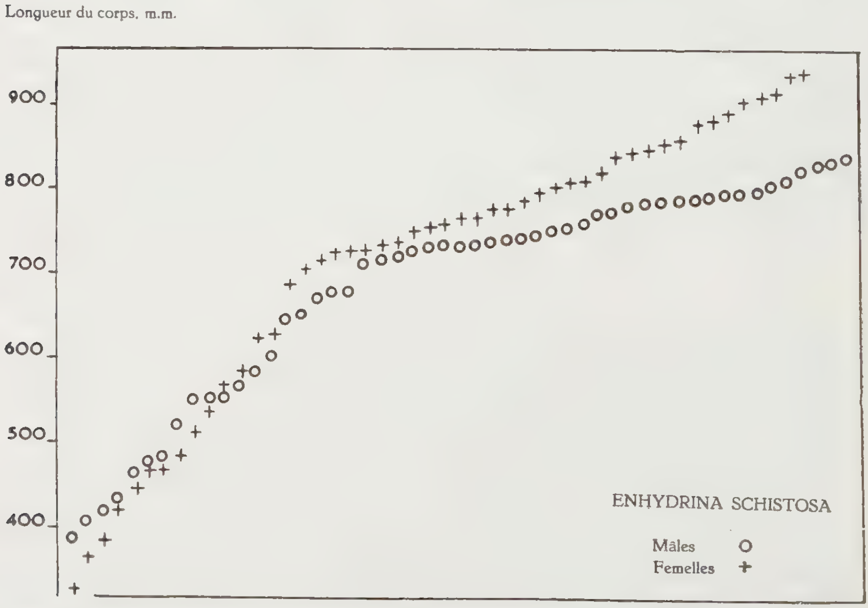

Fig. 1. Les serpents *Enhydrina schistosa* placés par ordre de la longueur du corps.

Le nombre de grands œufs dans l'ovaire et celui des embryons par animal correspondent exactement: il y a de 5 à 9 œufs par animal, en moyenne 7 œufs.

En plaçant nos animaux dans l'ordre de grandeur (fig. 1) nous trouvons l'inflexion de la courbe de Galton entre 640 mm et 700 mm et peu au de là les lignes pour les deux sexes vont s'écarter l'une de l'autre. En considérant en outre les données de l'examen des femelle senceintes, nous croyons pouvoir accepter une longueur de 650 mm tête et corps, comme longueur minimum pour l'adulte.

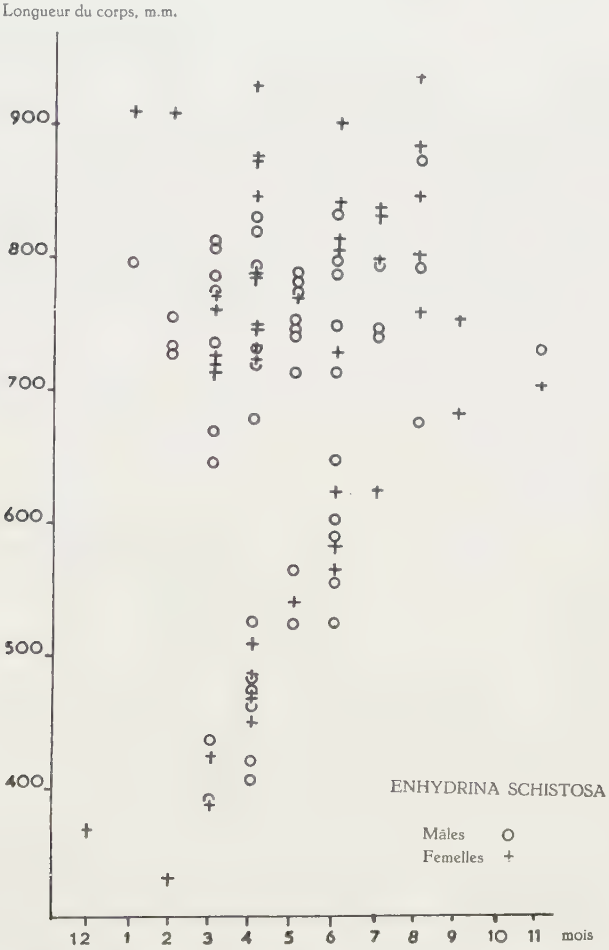

Fig. 2. Les serpents *Enhydrina schistosa* placés par ordre de la longueur du corps dans les mois où ils ont été captures.

CROISSANCE

Si nous groupons nos animaux dans un tableau indiquant la taille de l'animal et le mois de sa capture (fig. 2), il est évident que les plus petits animaux sont pris en décembre et février, ensuite qu'aux mois de février, mars, avril et mai, il y a un hiatus dans la succession des différentes longueurs, qui en fait deux groupes séparés, ce qui est bien moins clair dans les mois suivants. On peut bien en conclure qu'il y a un groupe de nouveau-nés en décembre qui atteint la longueur minima du groupe adulte après une année. Les deux sexes offrent à cet égard la même répartition.

CORRÉLATIONS

En examinant notre série en tenant compte des reflexions enoncées ci dessus, nos 48 femelles comprennent 34 adultes et 14 jeunes animaux et nos 51 mâles comprennent 36 adultes et 15 jeunes animaux. Entre la longueur du corps et de la queue (fig. 3) il y a pour les groupes entiers une corrélation marquée: pour les mâles $r = 0{,}935$ ou $z = 1{,}70 \pm 0{,}14$; pour les femelles $r = 0{,}940$ et $z = 1{,}74 \pm 0{,}15$ (table I).

Pour la longueur du corps et le poids (fig. 4) ces valeurs sont pour

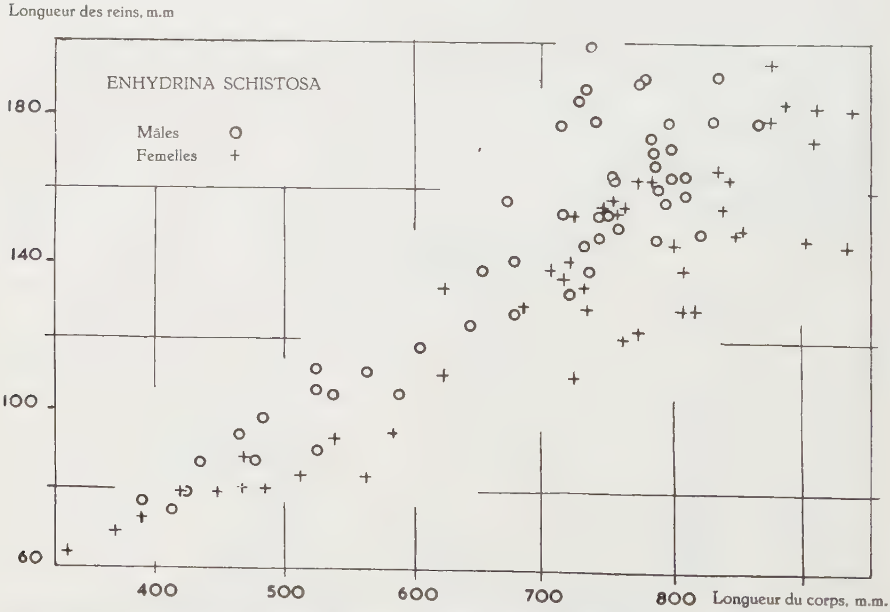

Fig. 3. La corrélation entre la longueur du corps et celle de la queue des *Enhydrina schistosa*.

les mâles $r = 0,920$ et $z = 1,59 \pm 0,15$. La différence n'est pas négligeable: $Dz/\sigma Dz = 2,7$.

Pour la longueur du corps et la longueur totale des glandes génitales (fig. 5) les corrélations sont du même ordre pour les deux sexes: pour les mâles $r = 0,800$ et $z = 1,08 \pm 0,14$; pour les femelles $r = 0,840$ et $z = 1,20 + 0,16$.

Entre les longueurs du corps et des deux reins r est pour les femelles (fig. 6) 0,970 et $z = 2,09 \pm 0,15$ et pour les mâles $r = 0,890$ et $z = 1,42 + 0,14$ ce qui indique une différence réelle: $Dz/\sigma Dz = 3,3$.

Quant aux données métriques elles-mêmes (tables II et III) la longueur du corps mesurée du museau à la cloaque indique un dimorphisme sexuel, les femelles sont plus longues: $D/\sigma D = 3,01$. Pour la longueur de la queue il y a une différence plus claire, mais en sens inverse: les mâles ont la queue plus longue en valeur absolue, et plus marquée encore si l'on considère la proportion du corps et de la queue,

TABLE I

Enhydrina schistosa

Corrélations ♂

	N	R	M ± σm	σ ± σσ	V ± σv
Corps	43	389–867	693,6 ± 20,1	131,8 ± 14,2	19,0 ± 2,0
Poids	43	35–323	194,0 ± 9,9	65,1 ± 7,0	33,6 ± 3,7
			r: 0,774	z ± σz: 1,04 ± 0,16	
Corps	51	389–867	685,0 ± 17,9	127,5 ± 12,6	19,0 ± 1,9
Queue	51	64–148	115,3 ± 3,4	24,3 ± 2,4	21,0 ± 2,1
			r: 0,935	z ± σz: 1,70 ± 0,14	
Corps	51	389–867	685,2 ± 17,9	127,5 ± 12,6	19,0 ± 1,9
Gonades	51	24–108	67,8 ± 3,2	23,0 ± 2,3	34,0 ± 3,4
			r: 0,800	z ± σz: 1,08 ± 0,14	
Corps	51	389–867	685,2 ± 17,9	127,5 ± 12,6	19,0 ± 1,9
Reins	51	74–190	143,8 ± 4,8	34,3 ± 3,4	24,0 ± 2,4
			r: 0,890	z ± ςz: 1,42 ± 0,14	
			♀		
Corps	42	330–938	704.7 ± 26,2	170,0 ± 18,6	24,2 ± 2,7
Poids	42	22–502	218,2 ± 19,1	123,5 ± 13,5	56,7 ± 6,2
			r: 0,920	z ± σz: 1,59 ± 0,16	
Corps	48	330–938	712,6 ± 23,8	164,7 ± 16,8	23,2 ± 2,4
Queue	48	48–142	103,2 ± 3,5	24,2 ± 2,5	23,5 ± 2,4
			r: 0,940	z ± σz: 1,74 ± 0,15	
Corps	43	330–938	734,3 ± 23,5	153,7 ± 16,6	20,9 ± 2,3
Gonades	43	20–191	114,6 ± 6,4	42,3 ± 4,6	36,8 ± 4,0
			r: 0,842	z ± σz: 1,20 ± 0,16	
Corps	47	330–938	711,3 ± 24,0	164,3 ± 17,0	23,0 ± 2,4
Reins	47	64–194	130,0 ± 5,2	35,6 ± 3,7	27,4 ± 2,8
			r: 0,970	z ± σz: 2,09 ± 0,15	

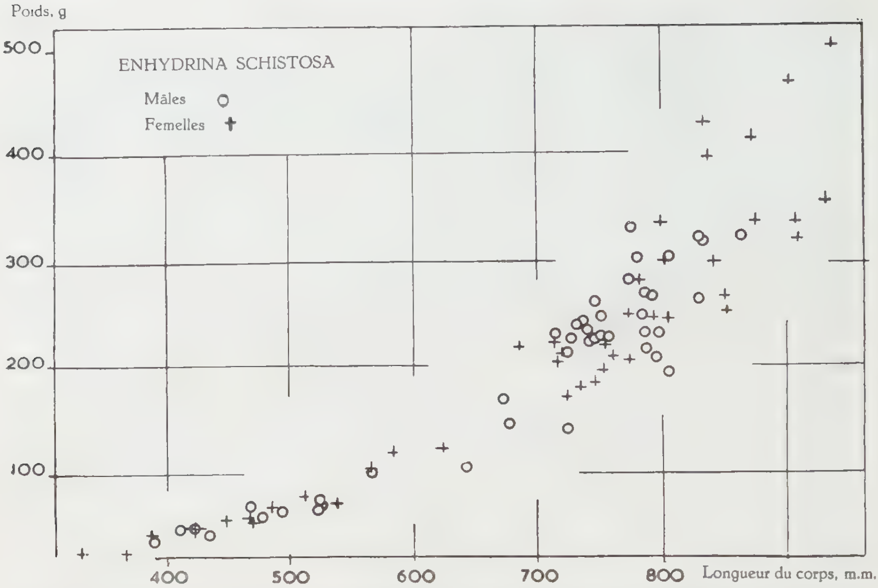

Fig. 4. La corrélation entre la longueur du corps et le poids des *Enhydrina schistosa.*

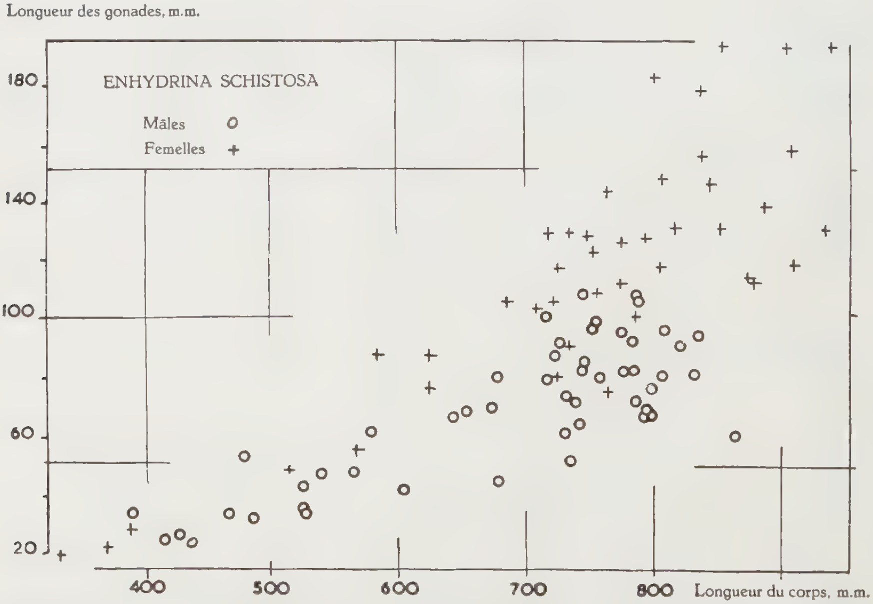

Fig. 5. La corrélation entre la longueur du corps et celle des deux glandes génitales des *Enhydrina schistosa.*

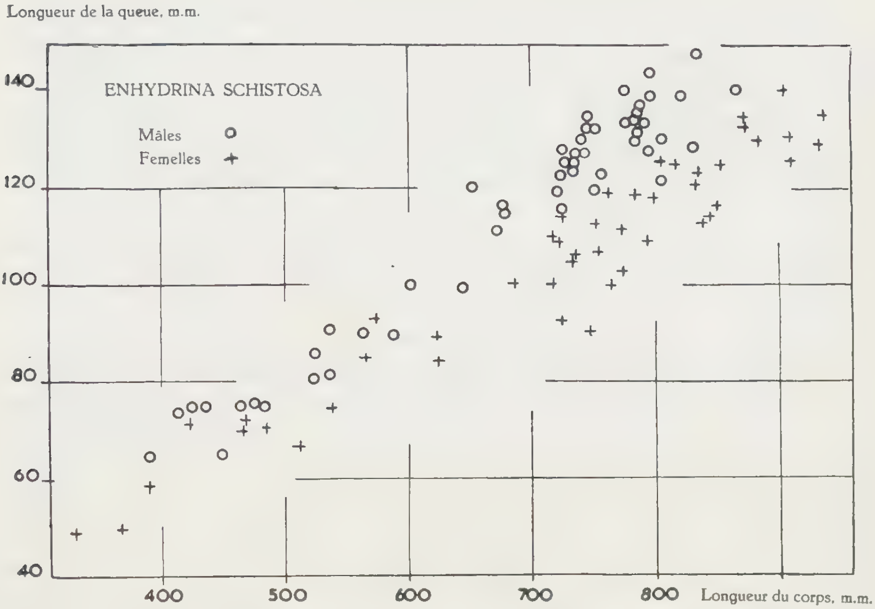

Fig. 6. La corrélation entre la longueur du corps et celle des deux reins des *Enhydrina schistosa*.

pour les mâles la queue compte $170^0/_{00}$ du corps et pour les femelles $140^0/_{00}$, la différence est $D/\sigma D = 5,2$. Pour le poids la différence n'est pas valable, $D/\sigma D = 2,2$ et pour autant que différence il y a, celle-ci se place probablement pour compte de la grossesse. En effet les 10 animaux aux grands œufs pèsent en moyenne 337,1 grammes, et les 19 autres femelles adultes en moyenne 257 grammes, un chiffre qui correspond fort bien avec celui des mâles: 245,6 grammes.

Comme il y a un dimorphisme sexuel dans la longueur du corps on peut s'attendre à retrouver des différences pareilles dans la plupart des données topographiques. En fait les chiffres de celles-ci à l'exception de celui de l'extrémité craniale des glandes génitales sont plus hauts chez les femelles, quoique le quotient $D/\sigma D$ n'excède la valeur trois que pour l'extrémité caudale de l'estomac. Il vaut mieux comparer les données de la topographie calculées en $^0/_{00}$ de la longueur du corps (fig. 7 et table IV). Là il n'y a pratiquement aucune différence: pour les organes dans la moitié craniale du corps, la position est un peu plus craniale chez les femelles, mais la différence, si elle est réelle, serait d'un ordre de grandeur de 2 à 3 % environ. Il n'y a que l'extrémité craniale de la glande génitale qui montre une différence notable: elle est plus haute chez la femelle (à $653^0/_{00}$ de la longueur) que chez le mâle oû elle se trouve à $697^0/_{00}$, une différence de 6 % environ.

Pour la longueur des organes il y a une différence très nette entre les glandes génitales des deux sexes (tables V et VI). La longueur des ovaires se rapporte à celle des testicules comme 3 à 2. Les reins aussi montrent quelque différence dans leur longueur proportionelle chez les deux sexes: à droite le rein mâle et femelle mesurent 97 et $110\,^{0}/_{00}$, à gauche 87 et $106\,^{0}/_{00}$ et les deux ensemble 184 et $216\,^{0}/_{00}$, une différence de 13/97 =13 %, 19/87 =20 %, et 30/186 =16 %.

Dans les deux sexes les glandes génitales à droite sont nettement plus longues que celles à gauche, chez les mâles $D/\sigma D = 3{,}7$ et chez les femelles 5,6.

Les reins à droite et à gauche ne donnent de différence statistiquement valable ni dans le groupe mâle, où $D/\sigma D = 1{,}4$, ni dans le groupe femelle avec $D/\sigma D = 2{,}3$ en valeurs absolues. Cependant dans les femelles les proportions sont assez différentes: le rein droit semble plus long: $97\,^{0}/_{00}$ de la longueur du corps, et à gauche $87\,^{0}/_{00}$, une différence de 10 %.

TABLE II

Enhydrina schistosa ♂

Données topographiques.

	M	N	R	M ± σ	σ ± σσ	V ± σ	σm^2
Longueur du							
Corps	760	36	652–867	760,0 ± 8,4	50,6 ± 6,0	6,6 ± 0,8	71,00
Queue	128	36	112–148	192,8 ± 1,4	8,6 ± 1,0	6,6 ± 0,8	2,06
Sommet du							
Coeur	323	36	274–379	322,6 ± 3,4	21,1 ± 2,5	6,6 ± 0,8	12,36
Foie	345	36	291–406	345,6 ± 3,3	19,7 ± 2,3	5,7 ± 0,7	10,80
Vésicule bil. . .	480	36	434–566	480,4 ± 5,3	31,5 ± 3,7	6,6 ± 0,8	27,60
Pancréas	490	36	435–578	490,0 ± 5,3	32,0 ± 3,8	6,5 ± 0,8	28,50
Rate	488	36	429–579	489,4 ± 5,3	31,8 ± 3,7	6,5 ± 0,8	28,50
Test. dr.	527	36	465–626	526,5 ± 6,3	37,7 ± 4,4	7,2 ± 0,8	39,60
Test. g.	568	36	498–664	568,5 ± 6,2	37,4 ± 4,4	6,6 ± 0,8	38,80
Rein dr.	593	36	519–689	593,9 ± 6,4	38,4 ± 4,5	6,5 ± 0,8	41,00
Rein g.	610	36	534–699	610,0 ± 6,2	37,4 ± 4,4	6,1 ± 0,7	39,00
Fin du							
Coeur	350	36	300–404	350,5 ± 3,5	21,0 ± 2,5	6,0 ± 0,7	12,25
Foie	476	36	408–551	476,0 ± 5,0	30,0 ± 3,5	6,3 ± 0,8	25,00
Vésicule bil. . .	497	36	440–587	497,4 ± 5,5	33,2 ± 4,0	6,6 ± 0,8	30,25
Pancréas	507	36	446–599	506,1 ± 5,4	32,5 ± 3,8	6,4 ± 0,8	29,00
Rate.	496	36	435–587	497,0 ± 5,4	32,6 ± 3,9	6,6 ± 0,8	29,50
Test. dr.	576	36	506–665	576,0 ± 6,8	39,6 ± 4,7	6,9 ± 0,8	46,50
Test. g.	600	36	525–685	601,4 ± 6,4	38,4 ± 4,5	6,4 ± 0,8	41,00
Rein dr.	675	36	591–778	675,5 ± 7,0	41,8 ± 5,0	6,2 ± 0,7	48,50
Rein g.	690	36	601–788	690,1 ± 6,6	39,9 ± 4,7	5,8 ± 0,7	44,00

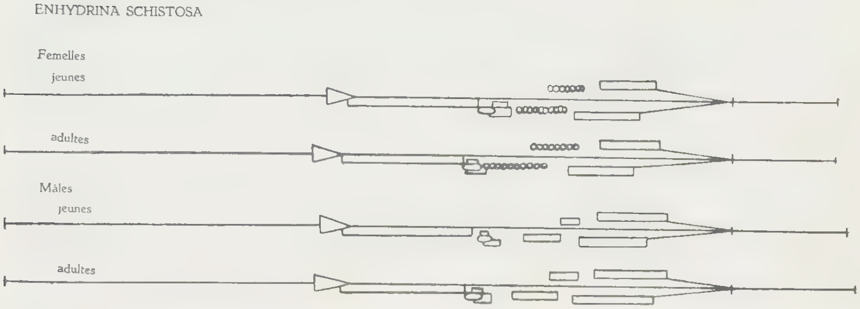

Fig. 7. Les données topographiques des serpents *Enhydrina schistosa* en promille de la longueur du corps.

TABLE III

Enhydrina schistosa ♀

Données topographiques.

	M	N	R	$M \pm \sigma$	$\sigma \pm \sigma\sigma$	$V \pm \sigma v$	σm^2
Longueur du							
Corps	804	34	685–938	803,3 ± 11,5	67,3 ± 8,2	8,4 ± 1,0	133,0
Queue	116	34	92–142	116,3 ± 2,2	12,6 ± 1,5	11,0 ± 1,3	4,7
Sommet du							
Coeur	340	34	276–397	338,8 ± 5,0	29,3 ± 3,6	8,6 ± 1,0	25,3
Foie	363	34	300–424	363,0 ± 5,6	32,5 ± 4,0	9,0 ± 1,0	31,0
Vésicule bil.. . .	503	34	415–596	503,6 ± 7,6	44,1 ± 5,0	8,7 ± 1,0	57,2
Pancréas	510	34	418–600	510,6 ± 7,5	43,7 ± 5,0	8,5 ± 1,0	56,0
Rate	509	33	418–597	505,5 ± 7,7	44,0 ± 5,4	8,7 ± 1,1	59,9
Ovaire dr. . . .	525	34	445–643	525,0 ± 8,7	50,4 ± 6,1	9,6 ± 1,2	75,0
Ovaire g. . . .	580	34	495–673	582,2 ± 9,2	53,6 ± 6,5	9,2 ± 1,1	84,5
Rein dr.	619	34	516–731	619,6 ± 9,7	56,5 ± 7,0	9,1 ± 1,1	94,0
Rein g.	653	33	557–760	653,6 ± 10,3	58,8 ± 7,5	9,0 ± 1,1	105,0
Fin du							
Coeur	367	34	301–426	367,4 ± 5,5	31,6 ± 3,9	8,6 ± 1,0	30,2
Foie	503	34	418–586	504,0 ± 7,2	42,0 ± 5,0	8,3 ± 1,0	52,0
Vésicule bil. . .	522	34	429–620	523,1 ± 8,2	47,7 ± 5,8	9,0 ± 1,1	67,0
Pancréas	529	34	432–621	531,3 ± 8,0	46,5 ± 5,6	8,8 ± 1,1	63,3
Rate	515	33	423–607	515,6 ± 7,8	44,7 ± 5,5	8,6 ± 1,1	60,5
Ovaire dr. . . .	601	34	500–713	599,7 ± 9,7	56,7 ± 7,0	9,5 ± 1,1	94,6
Ovaire g. . . .	634	34	545–734	635,9 ± 10,1	58,8 ± 7,2	9,2 ± 1,1	101,7
Rein dr.	697	34	589–821	700,5 ± 10,7	62,1 ± 7,6	8,8 ± 1,1	114,0
Rein g..	725	33	613–844	725,7 ± 11,1	64,0 ± 8,0	8,8 ± 1,1	124,0

Pour les intervalles entre les organes (tables VII et VIII) la question est plus compliquée: la distance B_1 du pancréas à la glande génitale droite est très nettement différente dans les deux sexes: D/σD =6,4; de même les distances B_3 du rein droit à la cloaque offrent une différance avec un quotient D′ςD =7,2. A gauche les distances C_1 du pancréas à la glande génitale ont une différence valide aussi avec D/σD =3,3, de même C_2 de la glande génitale au rein D/σD =11,— et l'intervalle C_3, du rein à la cloaque donne une différence avec D/σD = 3,2.

TABLE IV

Enhydrina schistosa

Plan topographique en $^0/_{00}$ de la longueur du corps

		♂		♀	
		Jeunes	Adultes	Jeunes	Adultes
M. corps		505	760	488	804
Corps		1000	1000	1000	1000
Queue		160	171	146	144
Coeur	sommet	432	425	440	421
	fin	470	462	477	456
	longueur	36	37	37	35
Foie	sommet	461	455	470	459
	fin	639	630	650	626
	longueur	176	712	176	178
Vés. bil.	sommet	646	630	650	626
	fin	668	655	672	650
	longueur	22	23	22	24
Pancr.	sommet	654	644	670	632
	fin	678	668	695	657
	longueur	24	23	25	25
Rate	sommet	650	641	669	631
	fin	661	654	680	641
	longueur	12	12	10	10
Gon. B.	sommet	710	697	700	653
	fin	761	760	770	749
	longueur	51	64	69	96
Gon. G.	sommet	760	750	749	720
	fin	788	791	795	787
	longueur	28	42	45	66
Les deux		79	106	114	161
Rein D.	sommet	788	780	779	770
	fin	885	891	870	865
	longueur	99	110	90	97
Rein G.	sommet	810	807	813	813
	fin	910	912	900	900
	longueur	95	106	87	87
Les deux		194	216	178	186

Le total des intervalles dans la moitié caudale à gauche, est nettement plus petit chez les femelles: $D/\sigma D = 5{,}6$, et encore la distance entre le pancréas et le rein gauche est nettement plus grande chez les femelles: $D/\sigma D = 4{,}7$.

TABLE V

Enhydrina schistosa ♂

Longueur des organes.

	M	N	R	$M \pm \sigma m$	$\sigma \pm \sigma\sigma$	$V \pm \sigma v$	σm^2
Corps	760	36	652–867	760,0 ± 8,4	50,6 ± 6,0	6,6 ± 0,8	71,00
Queue	128	36	112–148	129,8 ± 1,4	8,6 ± 1,0	6,6 ± 0,8	2,06
Coeur	27,6	36	20–34	27,3 ± 0,5	3,2 ± 0,4	11,4 ± 1,3	0,29
Foie	131	36	109–161	130,7 ± 1,8	11,0 ± 1,3	8,4 ± 1,0	3,36
Vés. bil.	17	36	6–32	16,8 ± 0,8	4,9 ± 0,6	33,8 ± 4,0	0,66
Pancréas	16,9	36	11–26	16,9 ± 0,6	3,2 ± 0,4	19,0 ± 2,2	0,37
Rate	8,7	36	4–14	8,7 ± 0,4	2,2 ± 0,3	25,3 ± 2,9	0,13
Testic. dr.	48,6	36	28–65	48,6 ± 1,4	8,3 ± 1,0	17,2 ± 2,0	1,92
Testic g.	32	36	17–47	31,7 ± 1,3	7,5 ± 0,9	23,7 ± 2,8	1,56
Les deux	80,5	36	45–108	80,8 ± 2,6	15,4 ± 1,8	19,1 ± 2,2	6,60
Rein dr.	83	36	64–106	83,3 ± 1,6	9,6 ± 1,1	11,4 ± 1,3	2,55
Rein g.	80	36	63- 93	80,2 ± 1,6	9,6 ± 1,1	12,0 ± 1,4	2,55
Les deux	162,5	36	127–190	163,2 ± 2,9	17,4 ± 2,5	10,7 ± 1,6	8,44
Poids		31	140–323	245,6 ± 8,6	48,0 ± 6,1	19,6 ± 2,5	74,00

TABLE VI

Enhydrina schistosa ♀

Longueur des organes.

	M	N	R	$M \pm \sigma m$	$\sigma \pm \sigma\sigma$	$V \pm \sigma v$	σm^2
Corps	804	34	685–938	803,3 ± 11,5	67,3 ± 8,2	8,4 ± 1,0	133,00
Queue	116	34	92–142	116,3 ± 2,2	12,6 ± 1,5	11,0 ± 1,3	4,70
Coeur	28	34	23–36	27,8 ± 0,6	3,3 ± 0,4	11,8 ± 1,4	0,32
Foie	143,	34	115–179	139,6 ± 2,6	15,0 ± 1,8	10,7 ± 1,4	6,62
Vés. bil.	19	34	12–29	19,2 ± 0,7	4,1 ± 0,5	21,4 ± 2,6	0,50
Pancréas	20	34	11–32	19,3 ± 0,9	5,1 ± 0,6	26,4 ± 3,2	0,76
Rate	8,5	33	3–15	9,0 ± 0,5	2,8 ± 0,3	31,1 ± 4,0	0,24
Ovaire dr.	77	34	55–119	76,8 ± 2,8	16,2 ± 2,0	21,0 ± 2,5	7,76
Ovaire g.	53	34	21–103	53,5 ± 3,2	18,5 ± 2,3	35,0 ± 4,3	10,00
Les deux	130	34	75–191	130,7 ± 5,3	30,8 ± 3,8	23,6 ± 2,9	27,90
Rein dr.	78	34	54–110	78,0 ± 2,0	11,8 ± 1,4	15,0 ± 1,8	4,20
Rein g.	70	33	56–88	71,9 ± 1,6	9,4 ± 1,1	13,0 ± 1,6	2,66
Les deux	150	33	110–194	150,8 ± 3,4	19,6 ± 2,4	13,0 ± 1,6	11,60
Poids	285	29	171–502	286,9 ± 16,3	88,0 ± 11,6	30,7 ± 4,0	267,00

Les proportions du plan topographique dans les animaux jeunes sont sensiblement les mêmes que chez les adultes: il n'y a que les dimensi-

TABLE VII

Enhydrina schistosa ♂

Intervalles entre les organes.

	M	N	R	M ± σm	σ ± σσ	V ± σv	σm^2
Museau-coeur	323	36	274–379	322,7 ± 3,5	21,3 ± 2,5	6,6 ± 0,8	12,30
Coeur-foie	–5	36	–10/+2	–4,8 ± 0,6	3,4 ± 0,4	70,0 ± 8,2	0,31
Foie-vés. bil.	4,3	36	–9/+26	4,2 ± 1,0	6,3 ± 0,8	85,7 ± 10,0	1,10
A	332	36	294–392	331,0 ± 3,7	22,2 ± 2,6	6,8 ± 0,8	13,70
Pancr.-test./dr.	21	36	2–45	20,6 ± 1,4	8,8 ± 1,0	42,6 ± 5,0	2,08
Test./dr.-rein/dr.	16,5	36	–2–40	17,8 ± 1,5	8,9 ± 1,0	50,0 ± 5,8	2,18
Rein/dr.-cloaque	85	36	61–104	84,9 ± 1,8	11,1 ± 1,3	13,6 ± 1,5	3,40
B	122	36	86–147	123,0 ± 2,8	16,6 ± 2,0	13,5 ± 1,6	7,67
Pancr.-test./g.	62	36	42–90	62,4 ± 1,8	10,5 ± 1,2	16,8 ± 2,0	3,05
Test./g.-rein/g.	9	36	–3–31	8,9 ± 1,3	7,5 ± 0,9	8,4 ± 1,0	1,56
Rein/g.-cloaque	71	36	51–84	70,8 ± 1,5	9,2 ± 1,1	12,9 ± 1,5	2,33
C	144	36	105–181	142,0 ± 3,0	17,8 ± 2,1	12,4 ± 1,5	8,80
A + B	454	36	380–532	454,8 ± 5,5	33,0 ± 3,9	7,3 ± 0,9	30,00
A + C	476	36	399–540	475,0 ± 5,8	35,0 ± 4,1	7,4 ± 0,8	34,00
Pancr.-rein/dr.	86	36	55–111	86,0 ± 2,1	13,0 ± 1,5	15,1 ± 1,8	4,40
Pancr.-rein/g.	103	36	76–134	102,7 ± 2,3	13,6 ± 1,6	13,2 ± 1,5	5,14

TABLE VIII

Enhydrina schistosa ♀

Intervalles entre les organes.

	M	N	R	M ± σm	σ ± σσ	V ± σv	σm^2
Museau-coeur	340	34	276–397	338,8 ± 5,0	29,3 ± 3,6	8,6 ± 1,0	25,3
Coeur-foie	–4,5	34	–14/–1	–4,4 ± 0,6	3,6 ± 0,4	80,7 ± 9,8	0,37
Foie-vés. bil.	0,3	34	-20/+28	0,9 ± 1,7	9,8 ± 1,2	1080 ± 132,0	2,80
A	335,0	34	272–410	335,8 ± 6,0	34,7 ± 4,3	10,3 ± 1,3	35,40
Pancr.-ov/.dr.	5,0	34	-22/+26	4,6 ± 2,0	11,7 ± 1,4	257,0 ± 31,0	4,04
Ov./dr.:rein/dr.	18	34	–5+49	17,3 ± 2,0	11,7 ± 1,4	67,5 ± 8,2	4,00
Rein/dr.-cloaque	106	34	82–130	105,1 ± 2,0	11,9 ± 1,5	11,3 ± 1,4	4,20
B	129	34	85–186	129,0 ± 3,6	20,9 ± 2,5	16,2 ± 2,0	13,00
Pancr.-ov./g.	51	34	22–95	51,4 ± 2,9	16,8 ± 2,0	32,7 ± 4,0	8,30
Ov./g.-rein/g.	–18,4	33	–50/+5	–18,1 ± 2,0	11,5 ± 1,4	64,0 ± 8,0	4,00
Rein/g.-cloaque	79	33	60–103	79,0 ± 2,0	11,5 ± 1,4	14,6 ± 2,7	4,00
C	111	33	66–165	111,0 ± 4,6	26,7 ± 3,4	24,1 ± 3,0	21,60
A + B	463	34	369–579	463,6 ± 7,5	44,1 ± 5,5	9,5 ± 1,2	57,20
A + C	429	33	356–541	445,7 ± 8,8	50,3 ± 6,2	11,3 ± 1,5	77,00
Pancr.-rein/dr.	89,8	34	65–139	89,6 ± 3,3	19,2 ± 2,3	21,4 ± 2,6	10,80
Pancr.-rein/g.	122	33	83–175	122,8 ± 3,6	21,1 ± 2,6	17,3 ± 2,1	13,50

ons des glandes génitales qui augmentent chez les adultes, et la situation des organes de la moitié antérieure qui devient plus craniale dans les adultes des deux sexes.

VARIABILITÉ

Pour les données topographiques chez les adultes, le coefficient de variabilité est petit: de 5,8 à 7,2 pour les mâles et de 8,4 à 9,6 pour les femelles.

Le poids est plus variable, V =20 pour les mâles, et 30 pour les femelles. Les longueurs des organes sont un peu plus variables aussi: le coeur, le foie, les reins ont un coefficient de 8,4 à 12 pour les mâles, et de 10,7 à 15 pour les femelles; les petits organes: pancréas, vésicule biliaire et rate ont V =19 à 34 pour les mâles, et de 21 à 31 pour les femelles, les glandes génitales ont V =17 à 24 pour les mâles et de 21 à 35 pour les femelles.

Les intervalles montrent une variabilité beaucoup plus grande: chez les mâles la distance A_2 du coeur au foie, A_3 du foie à la vésicule biliaire, B_1 du pancréas au testicule droit et B_2 du testicule droit au rein droit ont V =de 42 à 85. Chez les femelles l'intervalle A_2 du foie à la vésicule biliaire est excessivement variable, de telle façon que le chiffre n'en donne plus une image claire. D'ailleurs la distance B_1 du pancréas à l'ovaire droit est très variable aussi avec V =257. Enfin B_2 de l'ovaire droit au rein droit et C_2 de l'ovaire gauche au rein gauche ont des valeurs pour V de 67 et 64.

Amsterdam, août 1954

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ANNUAL REPORT
OF THE ZOOLOGICAL STATION
OF THE
NETHERLANDS ZOOLOGICAL SOCIETY
FOR THE YEAR 1953

As in previous years, the scope of the work done at the Zoological Station has covered mainly ecological problems, and the students' increased interest in these matters has certainly contributed to this year's progress. The line of research at Den Helder tends to show a markedly different development in comparison with the early years after its initiation. When the research program that had been initiated in the thirties got under way, the investigations undertaken aimed at a general orientation. At that time special attention was paid to the local distribution of certain animal species and to the underlying principles. In dealing with the causes of distribution it was customary to refer mainly to external, especially abiotic milieu factors. Gradually, however, another stage has set in, in which the study of the environment no longer predominates, but stress is rather laid on the animal's reactions to its environment. The line of research was thereby virtually switched over to physiology and ethology, although the problems remained ecological in essence. Part of the work, which is now being carried out, should be regarded from this point of view.

The investigation of the spatfall of the mussel *(Mytilus edulis)* was continued by Mr. van Dongen and Mr. van Haaften (both from Utrecht) and Mr. Bas (from Leiden). The work of van Dongen and van Haaften was a continuation of the attempt undertaken by Mr. Rooth in 1952. In the preceding annual report it was stated that the very youngest spat mainly settle on algae and hydroids, but that after a certain amount of time they leave these and join the old musselbanks or found new ones. Now, it is likely that the depth, at which the spat find themselves when settling, depends on light intensity. In this connection the question arises whether the youngest spat, which settle preferably in very shallow water, require more light than the young mussels that shift over from the algae to the banks and apparently settle deeper than the youngest spat. Therefore, data are now required on the settling at various depths, and it is a laborious job to obtain these. Hence, like Mr. Rooth in 1952, Mr. van Dongen and Mr. van Haaften did not obtain decisive results. We hope that the work will be resumed in 1954, however.

Mr. Bas continued his 1952-observations concerning the settling of young mussels on old banks, the foundation of new banks and the growing up of the spat. His participation in the Station's activity has come to an end for the time being. His records comprise interesting details on the settling and shifting of the young on certain banks, which will be published in the "Archives".

Mr. Bas also terminated his experiments on the influence of light and darkness on the duration of life of young cockles and mussels already mentioned in the previous report. His results show that under experimental conditions the mortality of mussels and cockles after settling is not enhanced by darkness to any appreciable degree. Since the spat because of their need for high light intensities cannot but settle in shallow water, whereas mussels, when adult, are apparently not adversely influenced by absence of light, it may be queried whether for the grown-up specimens there is an additional advantage in settling in shallow water. It is assumed that, at least for the cockles, the shallow position may favour the perception of the approach of enemies. It is known that the cockle has well-developed eyes.

Our knowledge of nudibranch slugs entered a new phase thanks to the work of Mr. de Wolf and Mr. van Haaften. The work of Mr. de Wolf was directed by Prof. ten Cate and Dr. de Wilde (Amsterdam). This investigation aimed at the localisation of smell and current perception in *Aeolidia papillosa* and *Cratena aurantia*, for which purpose sea anemones and hydroids were used as sources of scent. The chemoreceptors are situated in the rhinophores, whereas the sense of touch must be attributed to the oral tentacles. The rhinophores are not instrumental in the perception of currents; the localisation of this sense still remained uncertain.

The work of Mr. van Haaften was a continuation of last year's endeavours of Miss de Koning (Utrecht), who attempted to demonstrate that in running water slugs do not rely on a gradient of scent for finding their food. It was found that a slug, once it has been activated by scent, will head against the current, thus being guided to the source of smell. The data will be published in the "Archives" and need no discussion in full here. The result elucidates the general principle that in the sea scent or other factors like temperature or salinity changes may have a clear *stimulative* effect, but that *orientation* is a matter of current direction.

The behaviour of the common shrimp *(Crangon crangon)* under a diminishing head of water was studied by Mr. Glas (Groningen). It is obvious that a species like the shrimp, which in summer mainly inhabits the Wadden Sea, should possess responsive faculties that guide the animal away from the tidal flats during the ebb-tide. This would require a reaction to the change in water level as well as a choice of direction determined by the current. Mr. Glas only dealt with the former, the response to the falling of the water level. He found that shrimp actually react to excessive shallowness by departure and he also found out in what way they perceive the falling of the water level. No further discussion will be given here, as his contribution will appear in the "Archives".

An investigation into the chemoreception of *Littorina obtusata*, formerly initiated by Mr. Ebbinge Wubbe and Mr. Barkman, was continued by Mr. van Dongen. It was ascertained that *Littorina obtusata* reacts positively to the scent of Fucaceae and that the attraction varies according to the species of algae. The snail's preference for different species, however, apparently accords only partly with its preference for these species as food.

Our knowledge of the feeding mechanism of mussels, which was so much promoted by Dr. Tammes during the previous season, was now enhanced in one respect. Miss Blokzijl (Groningen) tried to find out whether mussels, in waters with a high concentration of particulate matter, will reject a greater proportion of material (eventually taking up less) than in waters containing little matter in suspension. It has been a debated question for many years whether waters, teeming with suspended matter (plankton included), would be less favourable to the feeding of mollusks than those carrying relatively few particles. An attempt was made to solve the problem by separating faeces and pseudofaeces and to determine their relative quantities in waters of different silt content. It became evident that this quantitative relation indeed depends on the concentration of the medium, but individual differences are considerable. Since the results obtained so far are quite valuable it would be worth while to have these experiments continued.

Other investigations were undertaken by Miss Koopman (from Utrecht), Mr. den Hartog an Mr. Hillenius (both from Amsterdam).

Miss Koopman made some observations on the cardiac rhythm in young mussels. The heart seemed to undergo a marked retardation when the shells were closed, but the experiments will have to be continued in order to obtain more reliable results.

Mr. den Hartog studied the behaviour of two nudibranch slugs from the tidal flats, *Alderia modesta* and *Limapontia depressa*. The choice of this item was entirely due to his own interest in these species, which mainly feed on algae of the genus *Vaucheria*. His observations are of importance in connection with our experience with other nudibranch slugs. They are likely to be continued in 1954.

Mr. HILLENIUS visited Den Helder in order to check his observations on ciliary movement in *Metridium senile* previously made in Amsterdam. This investigation was directed by Prof. TEN CATE and Dr. DE WILDE (Amsterdam); the observations made at Den Helder only served to complete his material. He was able to confirm that ciliary reversal is induced by various substances, as was formerly described by PARKER. This phenomenon is most remarkable in connection with the irreversibility of ciliary activity in general.

Finally, mention should be made of the work of Mr. McKAY, an American Fullbright student, who stayed at Den Helder for almost a year. His activity concerned the annual migration of herring into the former Zuiderzee, more in particular the influence of external factors on the herring's first appearance. His material was based on the records of landings from 1880 to 1910 and the matter seems to resolve itself into the following. An annual periodicity in reproduction, induced by increasing temperature or daylength, should be considered the underlying principle. Superimposed on this rhythm there is the influence of temperature during a certain part of the winter, which determines whether reproduction will start early or late. The moon in its turn limits the earliest date of arrival to a certain range of its cycle, within which some shifting may again be caused by the actual temperature within that period. The matter is therefore complicated enough and the results cannot be accepted without reserve until the data have been studied in more detail. Valuable help was given by Prof. S. W. VISSER of the Royal Netherlands Meteorological Institute, De Bilt.

In connection with the foregoing details the work of Mr. DE BLOK should be mentioned. Thanks to a grant made by the Netherlands Organization for Purely Scientific Research (Z.W.O.) he was given a research assignment for investigations into lunar or tidal influence on reproduction in marine animals, as was already put on record in the previous annual report. In 1953 his energies were mainly devoted to orientation and preparation and it will still take considerable time before the installation apparatus designed will work to perfection. The execution of this research is directed by Dr. KORRINGA and the undersigned.

Apart from his main commission comprising problems connected with waste water disposal, which will be discussed later on in this report, Dr. TAMMES found time to study the development of gas in the airbladders of *Ascophyllum nodosum*; his experience has contributed to a better understanding of known facts. Under natural conditions the oxygen content and pressure of the gas depends on the intensity of photosynthesis, and the oxygen liberated inside the bladder may in part be exchanged for nitrogen dissolved in the water outside. Loss of gas in the bladder may either be caused by diffusion or by respiration. When loss exceeds production the gas pressure will at a given moment be reduced below the pressure of the medium and the airbladders will then tend to deflate. The elasticity of the bladder wall will oppose the deformation with the effect that water enters the cavity. It was demonstrated that the bladder walls are permeable for gases, water, various salts and sugars. Details have been published in "Acta Botanica Neerlandica", **3**, 114–123, 1954.

Dr. WESTENBERG has several times given a review of the overfishing problem. This year a Dutch version, revised with regard to recent literature, has appeared in "Statistica", **7**, 71–95, 1953. Another point that has his particular interest concerns the reactions of fish to natural sound signals. A contribution to this subject was published in "Journal du Conseil", **18**, 311–325, 1953. In connection with the desiderata raised by his suppositions the Netherlands Organization for Applied Research (T.N.O.) has developed a hydrophone sensitive to a wide range of frequencies.

As in former years, Mr. KRISTENSEN spent much of his time on the study of migrant species by means of our system of buying up landed specimens. The bream *(Brama raji)* was conspicuous by its absence in 1953, in striking contrast to the considerable invasion of this species witnessed in previous years. The large numbers of haddock *(Gadus aegle finus)* met with in 1953 were interesting, since the species hardly occurs in the southern part of the North Sea apart from periods of abundance as witnessed immediately after the world wars. Mr. KRISTENSEN assumes a connection between this year's increased occurrence of haddock and the excessive penetration of Atlantic waters into the southern North Sea from the North, which was at that time observed by the German research vessel "Gauss". Apparently, this penetration of Atlantic waters did not stop the immigration of southern species through Dover Strait, since the red gurnard, *Trigla cuculus*, which was rare in 1952, was numerous in 1953. It is remarkable, however, that the southern migrants, entering the North Sea through Dover Strait, arrived late in the season. Since the most important 1953-migration data are listed below, they are not further discussed here.

The hydrographic investigations under the direction of Mr. POSTMA mainly concerned the cycle of nutrients in the Wadden Sea. The chemical analysis of suspended matter is a laborious business, which is steadily proceeding thanks to the patience of Mr. BEKE. A series of

Species	Sex; Size (cm)	Locality
(LV = Lightvessel; ST means buoy on the Silverpit-Texel route)		
Southern migrants, supposed to have entered the North Sea through Dover Strait		
Alopias vulpes	± 150	from fyke, Texel island
Raia brachyura		between Texel Hole and Silver Pit
Raia montagui		between coastal waters and Silver Pit
Acipenser sturio	16 and 55 kg	near ST 3; N. of Terschelling, 33 m
Clupea pilchardus		near LV "Texel", from Texel Hole and Tea Kettle Hole
Merluccius merluccius	♂♂ 53–58	near ST 4 (2 sp.), Texel Hole, Black Bank
Hippocampus europaeus	14	Mouth of the Ems
Spondyliosoma cantharus	6; 16–35	smallest sp. from Wadden Sea, the others from Texel Hole-Tea Kettle Hole
Atherina presbyter	7–13	1 sp. from fyke near Den Helder, 9 sp. from brackish waters on Texel
Trigla cuculus		mostly from Texel Hole area (no data collected in August)
Solea lascaris	25 and 27	60 KM WNW of IJmuiden
Northern fishes likely to have entered the southern North Sea from the North		
Gadus virens	1 ad. + 4 juv.	ST 4 (1 ad. sp.); from fykes near Den Helder (4 sp. ± 20 cm)
Molva molva	30–35	Texel Hole – ST 5
Onos cimbrius		Texel Hole area
Anarhichas lupus	35–50, 75	SW border of Oyster Grounds (4 sp.); Black Bank (1 sp. 75 cm)
Fishes, whose direction of migration is uncertain		
Maurolicus mulleri	6	washed ashore at Texel
Raniceps raninus	7 and 27	near Texel; Texel Hole
Labrus berggylta	♀ 32.5	90 KM WNW of IJmuiden
Crenilabrus melops	15 and 16	from fykes near Den Helder
Scorpaena dactyloptera	8, 9, 16, 15	ST 3 (2 sp.); Texel Hole (2 sp.)
Lepidorhombus whiff-iagonis	♀ 47	near LV "Texel"
Zeugopterus punctatus	17	Texel Hole
Aphia pellucida	5.5	Wadden Sea
Evertebrates, "rare" in the area off Den Helder		
Portunus puber		coastal waters (3 sp.); LV "Texel"; Texel Hole (7 sp.); ST 2
Portunus depurator		near ST 4
Ebalia cranchi		Texel Hole
Diogenes pugilator		Texel Hole (in *Clathrus*- and *Lora*-shells).
Nephrops norvegicus		Texel Hole – ST 4
Pecten maximus	13, 14, 14	Pit-buoys P2–P4
Eledone cirrhosa		LV "Texel" – Tea Kettle Hole
Octopus vulgaris	2 ♀♀	Texel Hole; ST 5
Sepia officinalis	20 sp. < 13 cm	mostly from coastal waters
Loligo vulgaris		mostly from coastal waters (no data collected in Aug.–Sept.)
Loligo forbesi		mostly from Texel Hole area (no data collected in Aug.–Sept.)

Numbers per month											
J	F	M	A	M	J	J	A	S	O	N	D
—	—	—	—	—	—	1	—	—	—	—	—
5	5	1	1	3	—	—	—	—	1	1	1
9	2	2	4	1	4	—	—	1	3	12	10
—	—	—	—	—	—	—	—	—	1	—	1
—	—	—	—	8	10	—	—	—	—	1	—
—	—	—	—	1	2	1	—	—	—	—	—
—	—	—	—	—	—	—	1	—	—	—	—
—	—	—	—	—	—	—	—	4	5	2	2
—	—	—	—	—	10	—	—	—	—		—
1	—	1	1	23	397	208	?	1	1	7	1
—	2	—	—	—	—	—	—	—	—	—	—
—	—	1	—	—	—	—	—	4	—	—	—
—	1	—	—	—	—	—	—	1	2	—	—
—	—	11	1	2	—	—	—	—	—	3	—
—	—	5	2	—	—	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—
—	—	1	—	—	1	—	—	—	—	—	—
—	1	—	—	—	—	—	—	—	—	—	—
—	—	—	—	1	—	—	—	1	—	—	—
—	—	—	—	—	2	—	—	—	1	1	—
—	—	—	—	—	1	—	—	—	—	—	—
—	—	1	—	—	—	—	—	—	—	—	—
—	—	—	—	—	1	—	—	—	—	—	—
—	—	2	2	4	2	—	—	—	2	—	—
—	—	—	—	—	—	—	—	—	—	5	—
—	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	—	—	—	—	—	—	—	22
—	1	3	1	1	2	1	1	7	18	6	1
3	—	—	—	—	—	—	—	—	—	—	—
—	1	2	—	—	—	—	—	—	1	—	2
1	—	—	—	—	—	—	—	—	—	—	1
—	—	—	—	22	90	8	7	4	4	3	7
—	—	—	1	126	361	41	?	?	—	18	24
7	—	—	1	—	597	486	?	?	176	618	419

analyses of monthly samples from three stations between Den Helder and Den Oever is now available.

The salinity distribution within the Waddensea channels was studied in cooperation with the Royal Netherlands Meteorological Institute (K.N.M.I.), the Oceanographic Section of which has, in post-war years, developed a continuous recorder of temperature and salinity, to be used on board a running vessel (DORRESTEIN in: Meded. Verh. Kon. Ned. Met. Inst. **59**, 387–403, 1954). With this instrument Mr. POSTMA intends to investigate the formation and distribution of tiderips. Provisional measurements made by Dr. DORRESTEIN of the K.N.M.I. and Mr. POSTMA have already demonstrated its suitability for this purpose.

Besides, Mr. POSTMA cooperated in investigations carried out in the harbour of Ymuiden by the Government Institution of Fisheries Research, the Government Institution for the disposal of waste water, the Rijkswaterstaat and the Zoological Station. This investigation was started with a view to assessing the extent to which fish suffer from harmful substances in waste water discharged by nearby industrial plants.

Considerable attention was again paid to the deteriorated condition of the Nieuwediep, which formerly used to furnish the water for the aquarium of the Zoological Station. This matter is becoming rather critical. In connection with the construction of the new naval base the Nieuwediep has been closed, as was already mentioned in last year's annual report. Its marine state was then seriously affected, but good water could at first still be obtained from the deep. This year, however, silt and low salinity became a regular nuisance, so that water had to be shipped almost constantly from the Marsdiep. As long as the new harbour is still under construction it is hard to make predictions, but it seems likely that in the future a regular water supply from the Marsdiep will be indispensable for our aquarium.

Finally, Mr. POSTMA spent much time on working out his observations made during the geological expedition to the Caribbean area, already placed on record in the previous annual report, and some hydrographic data of the Snellius Expedition.

Bij October 1st Dr. TAMMES finished his investigations on the influence of industrial waste water on marine life. By this time we are free to state that this item was connected with industrial efforts to win potassium from seawater. In this procedure potassium is precipitated with the aid of a certain reagent which can only be recuperated in part. Thus the necessity of waste diposal led to the study of the reagent's toxicity and decomposition under natural conditions. In the two and a half years that he devoted to the subject Dr. TAMMES gained an understanding of the process of intoxication, the dependence of toxicity on temperature, the susceptibility of several species, the decomposition of the reagent under aerobic and anaerobic conditions, and its ready adsorption by organic matter. Part of the results concerning the dependence of toxicity on temperature will be published in "Physiologia Comparata et Oecologia". The investigation has yielded a reliable basis for assessing the risk involved in discharging this waste substance into the sea. Industries become more and more inclined to drain their wastes into the sea without realizing the need of precautions against the consequences. This attitude would, within a few decades, spoil our coastal waters if the Government should not intervene.

The number of students attending this year's summer courses amounted to 19; 10 of them were from Leiden, 8 from Utrecht and 1 from Amsterdam. On account of illness of the director the courses were given by Messrs. KRISTENSEN, POSTMA, TAMMES, WESTENBERG, and DE BLOK.

Apart from our own program Dr. KIPP organized courses for 1st and 2nd year students from Utrecht; 40 of them were split up into four groups, each group visiting the Station for three days. Also from the Free University (Amsterdam) 9 students came for 6 days under the direction of Mr. ANTHEUNISSE.

The total number of man-days for individual investigators and summer course participants in 1953 amounted to 1514. There is, from year to year, a striking variation in number, the average being 1016 for the period 1947–1953; in 1952 the number was 736, against 1514 in 1953. For this reason it is hard to state whether there is progress or decline, as was attempted in the previous report.

Close cooperation was again maintained with several public agencies, especially with the Government Institute of Fisheries Research and the "Rijkswaterstaat". On many occasions our Station was in touch with the University laboratories. Our special acknowledgments are due to Mr. VAN LIESHOUT, Commissioner of Pilotage at Den Helder, for his courtesy and helpfulness. The Netherlands Educational Film Company has, for several years, taken advantage of the Station's installation, and has, in exchange for facilities granted, kindly promised copies of the films made at Den Helder. The German research vessel "Gauss" again visited Den Helder in 1953. The investigations of the German Hydrographical Institute in the southern part of the North Sea are most interesting and again it was a privilege to have the work explained. The English research vessel "Sir Lancelot" called at Den Helder several times. Among the other foreign visitors we only mention Dr. B. H. KETCHUM of the Oceanographical Institute at Woods Hole (Mass., U.S.A.).

The building required considerable expenditure, especially for repairs in the caretaker's rooms. Other parts of the building were also improved during this and previous years, which has made things look a good deal better. The gale of February 1st caused rather serious damage to the roof. Finally, repairs of the seawater supply-piping through the dike were rather expensive.

The students' lodge "Potvis" (= Cachelot) has not cost a great deal this year. In summer it houses quite a number of students and we only wish it could accomodate twice as many.

The Station's vessel "Max Weber" did not require much either after last year's replacement of her crank-shaft. Mr. VAN BREDA, the new skipper, gave her a general overhaul, which restored her good appearance. The vessel spent 56 days at sea during the year; she is quite indispensable for the Station's ecologic and hydrographic activities. The rowboat "Pelk"[1] underwent thorough repairs at the end of the season.

There have been some changes in personnel during the past year. In the first place Dr. TAMMES finished his investigations on waste water influence, carried out by contract with Mekog Ltd., Ymuiden, on October 1st. His departure was felt as a severe loss since we all benefited from his dexterity in experimental technique. Dr. TAMMES joined the staff of the Phytopathological Service at Wageningen. Mr. G. VAN DER WAL, student analyst, equally working for Mekog, was taken over by the Station. He stepped into the place vacated by the student analyst T. DE BOER, who was appointed analyst at the Government Institution of Fisheries Research. Miss C. NAGTEGAAL left for Australia; she was succeeded by Miss C. M. PLANKEN. Mr. C. K. A. VAN BREDA was appointed resident caretaker-skipper; together with his wife he moved into the Station on June 1st. Finally, mention should be made of the director's absence for three months on account of illness. Fortunately his administrative and scientific activities went on for the greater part during this period.

The Library gained a further extension of exchange relations. It is clearly noticeable that the staff of the Station can avail themselves of the services of a librarian of scientific training in the person of Dr. WESTENBERG, who is specially detailed for the purpose. He and Miss STOLL together settle quite a lot of affairs, which would have remained undone in the absence of a special worker.

The supply of study materials again scored a considerable turnover. The purchases of animal specimens amounted to about fl. 3300.—, while fl. 450.— were spent on freight, packing, preserving solutions, etc. The expenditure, including amounts paid for specimens for our own use and aquarium food, totalled fl. 3750.—. The income amounted to fl. 4500.—. Hence the profit realized was about fl. 770.—. This part of the affairs, and especially the study of the specimens received, is in the hands of Mr. Kristensen, assisted by Mr. Buhre.

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[1] This boat has been named "Pelk" in memory of TER PELKWIJK, a promising junior biologist, who was killed in action south of Java in 1942.

The Government grant for 1953 amounted to fl. 74,550.—, of which fl. 60,000.— was destined for salaries and National Insurance, the remaining part for the Station's exploitation. The further income consisted of the Society's contribution to the library and to the publishing of her periodical, some 300 copies of which are used for exchange. For 1953 there was, moreover, an extra-sum from the National Rehabilitation Fund. Thus the Station's income totalled over fl. 80,000.—. The budget is likely to call for another fl. 10,000.— in 1954. The status of the Zoological Station has gradually changed, so that its new function in Holland should justify increased expenditure. The statement of income and expenses is appended.

Statement of Income and Expenses

Income		Expenses	
Government grant	fl. 74,550.—	Salaries	fl. 54,587.62
Grant from Roy. Netherl. Bot. Society	,, 100.—	Auditing	,, 532.50
Contribution to salaries from Reservefund	,, 500.—	Contribution to National Insurance	,, 5,659.18
Contribution from National Rehabilitation Fund	,, 1,213.46	Rates, taxes, and insurance	,, 1,219.24
Study Material	,, 4,516.40	Lighting, heating, telephone	,, 3,888.84
Staff contribution to Pensionfund	,, 1,984.95	Buildings & furniture	,, 3,868.59
Sickness Benefit	,, 258.57	Ships & nets	,, 2,139.01
Contribution for Library from the Society	,, 300.—	Instruments, glass utensils, chemicals	,, 1,964.42
		Fitting shop	,, 541.54
		Study materials	,, 3,745.91
		Postage, freight, packing, writing & drawing materials	,, 1,272.32
		Library	,, 1,241.15
		Travelling expenses	,, 234.10
		General	,, 90.52
		Pension fund	,, 1,984.95
		Balance in hand	,, 453.49
Total	fl. 83,423.38	Total	fl. 83,423.38

Den Helder, February 1954
J. Verwey

ASPECTS AND PROSPECTS OF THE CONCEPT OF INSTINCT

(VICISSITUDES OF THE HIERARCHY THEORY)

by

A. KORTLANDT[1]

(*Zoological Laboratory, University of Amsterdam*)

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In recent years an old field of research, the hierarchy of instincts, has been rediscovered by students of behaviour. Most of these recent workers, however, seem to be unaware of the progress that has already been made by many predecessors in this field, and some of them go so far as to claim that the principle of hierarchy is exclusively the discovery of the school of workers to which they happen to belong. In his book

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[1] In this paper some results achieved by the Dutch "Research Group on the Behaviour of Domestic Animals" (T.N.O.) have been inserted. The author wishes to express his sincere thanks to Dr. W. H. THORPE, Miss E. M. BARRAUD and Miss D. R. HAINES who have given much careful help in correcting the English text. The author also wishes to extend his thanks to the Institute of Psycho-Analysis, London, for the English quotations from the works of FREUD.

"The Study of Instinct" TINBERGEN (1951, p. 104) writes: "The principle of hierarchical organization has been tested in but three cases: the digger wasp, the three-spined stickleback and the turkey", thereby referring to papers by BAERENDS (1941), TINBERGEN (1942), and RÄBER (1948). Similar statements explicitly excluding the contributions of other and previous schools have been made by HINDE (1953, p. 189; 1954, p. 44), LORENZ (1952, p. 54; 1954, p. 140), and RÄBER (1948, p. 249). As a matter of fact, however, the concept of hierarchy has had a long history.

One could understand the boldness of such statements as quoted above if these modern workers had succeeded in developing a new way of approach to the problem by means of which the many pitfalls in this field might be avoided and a new basis for the concept of hierarchy be laid. A critical examination, however, will show that the logical consequences of these newer ideas on hierarchy have not been considered by their exponents and, moreover, the older concepts appear to contain valuable elements which are still worthy to be preserved as they may present useful suggestions for new investigations. This is especially important because in actual scientific research it often happens that general theory determines which facts shall be observed, instead of the observed facts determining which theories shall be developed. We shall see that this state of affairs applies also to the history of scientific ideas on hierarchy.

In this paper a review of existing ideas on hierarchy will first be given. It will be seen that in the past, as in the present, many preconceived views have seriously hampered the recognition of the principle of hierarchy. Also, the criteria of evidence pointing to a hierarchical organisation of behaviour will be critically examined, and as a consequence of this a part of the criteria that have been applied by some recent workers will be rejected. Finally, some prospects of future research will be envisaged.

I. THE IDEA OF HIERARCHY IN PSYCHOANALYTICAL AND CHILD PSYCHOLOGY

FREUD's *approach to hierarchy*

It is interesting to note that the principle of hierarchical organisation in behaviour has been known for half a century or even longer. In 1905 the first edition of FREUD's "Drei Abhandlungen zur Sexualtheorie" was published. (Ges. Werke V, pp. 33–145; English editions: "Three Contributions to the Theory of Sex", 1910; "Three Essays on the Theory of Sexuality", Standard Ed. VII, pp. 125 245, 1953) In this pioneering booklet FREUD presented a detailed account of his views with regard to the organisation of the subordinate or partial instincts ("Partialtriebe") under the supremacy of the genital instinct ("Genitaltrieb") and with regard to the ontogenetical development of this hierarchical system[1]. In doing so FREUD continued and extended the work of several previous pioneers such as HAVELOCK ELLIS, M. HIRSCHFELD, VON KRAFFT-EBING, MOLL, and others whose names are still well-known today even in lay circles and whose main writings have been reprinted regularly in recent years (e. g. VON KRAFFT-EBING in 1952). It may be that these authors in their turn had predecessors who are forgotten now. FREUD's quotations in this connection go back to GLEY (1884) and JEAN JACQUES ROUSSEAU (1712 1778).

Moreover, one may safely assume that FREUD was inspired by parallel ideas in neurology at that time. Since JACKSON's famous "Croonian lectures on evolution and dissolution of the nervous system" (1884) the concepts as well as the terms "hierarchy" and "level" of nervous centres have been familiar to anybody dealing with nervous diseases.

It is quite impossible to summarise FREUD's findings on hierarchy in a few pages and therefore any student of animal behaviour who is interested in the fundamentals of this science must read the original paper quoted above, amplified by some other writings by the same author. (Especially "Triebe und Triebschicksale", published 1915, Gesammelte Werke X, pp. 210-232, English translation: "Instincts and their vicissitudes", Collected Papers IV, p. 60ff, further "Die infantile Genitalorganisation", published 1923, Ges. Werke XIII, pp. 293-298, English translation: "The infantile genital organization of the libido", Collected Papers II, p. 244 ff.) Some aspects of psychoanalytical theory, however, must be mentioned here and reviewed briefly in order that the tenor and coherence of this paper may be properly understood.

First, it is important to realise that FREUD studied hierarchy by studying ontogenetical development as well as adult organisation of instinctive driving forces. During ontogeny the partial instincts mature, are conditioned, and function more or less independently of each other for some time before they are integrated into larger units, and these larger units in their turn remain independent for some time until, as a consequence of further maturation, they join together as components in a still higher unit of organisation, and so on. This sequence justifies the recognition of developmental stages or phases in instinctive organisation, viz. the oral phase, the anal-sadistic phase, the phallic phase and the genital phase, corresponding with as many hierarchical levels in the driving system of "sexual" behaviour. (In this context we may leave out of consideration the special connotation of the word "sexual" in Freud's terminology.)

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[1] In the official English edition of FREUD's collected papers "Trieb" has been translated "instinct", although in many cases the term "drive" would have been more adequate. The word "Trieb" has both connotations.

It will be clear that this two-sided approach to hierarchy (ontogenetic development as well as adult organisation) offers great possibilities for analysing the interactions in the driving system, both during the period when the drives under consideration are still working functionally independently and during the period when they have been integrated into a comprehensive instinct of higher level. It was Freud who in this way (thirty years before von Holst and Lorenz) recognised endogenous action-specific stimulus generation in a fixed motor pattern, viz. in false-sucking (Wonnesaugen), if we translate his findings into ethological terminology (Ges. Werke, V, pp. 80-81; Stand. Ed. VII, p. 180). No doubt Freud's ideas on this point were largely influenced by the theory of "specific energies" of Johannes Müller who was one of Freud's teachers. In this connection Freud's definition of instinct (Trieb) may be quoted: "By an 'instinct' is provisionally to be understood the psychical representative of an endosomatic, continuously flowing source of stimulation, as contrasted with a 'stimulus', which is set up by single excitations coming from without." (Ges. Werke V, p. 67; Stand. Ed. VII, p. 168) This concept differs little from the von Holst-Lorenz-Tinbergen theory of hierarchically organised nervous centres which are supposed to produce internal stimuli. The resemblance goes even further; for example, the goal of an instinct is defined as "the act towards which the instinct tends", i. e. a consummatory act (Ges. Werke V, p. 34; Stand. Ed. VII, p. 136).

Six major points in Freud'*s theories*

Now let us consider some major points in Freud's doctrines bearing on the problem of hierarchy of instincts.

1. During the initial stage of their development, subordinate instinctive drives are on the whole neither elicited by a specific object (i.e. a person or class of persons) nor directed towards a specific goal ("Ziel", i. e. a consummatory act). In the beginning these instinctive urges only represent rather unshaped and uncanalised amounts of nervous energy, the sources of which are largely aroused in connection with ("in Anlehnung an") vital bodily functions to which these sources are attached. (Anaclitic type of instinct development.) For example, non-sexual food sucking in a baby promotes the first arousal of libidinous ("sexual") oral drives. (Cf. "priming" and similar processes dealt with in Chapter IV, § 3, of the present paper.) Other subordinate instincts, however,

mature spontaneously without being aroused by stimulating factors.

2. During the following stage of their development all these subordinate instincts become more or less irreversibly conditioned to an object ("object-finding" or "object-choosing", a process identical to "imprinting" in ethological terminology) and they find a motor outlet or goal by way of a satisfying activity. This development also proceeds often attached to other vital functions, i. e. according to the anaclitic type. Hence, due to her physical attentions, the mother represents the first sexual object for the child in the same way as the parent (or foster-parent) of a newly hatched gosling serves as its first sexual object. Thus, strictly speaking, according to FREUD neither the objects nor the goals are assumed to be innate; although it is true they are in fact assumed to be largely preformed and predetermined by innate factors such as physical conditions, erogenous zones, primal phantasies, etc. Whereas object-finding in man can be paralelled to imprinting in animals, goal-finding perhaps finds its counterpart in such phenomena as have been described by KUO (1931, 1938), PADILLA (1935), HUNT (1941), NISSEN, CHOW and SEMMES (1951), BIRCH, and RIESS (quoted by LEHRMANN, 1953).

3. In general, different subordinate instincts mature, become conditioned and find their goals more or less independently of each other, and often at different ages (i. e. in different sensitive periods). This explains why normal infantile behaviour reveals many discrepancies, incongruities and aberrations, which fact gave rise to FREUD's peculiar characterisation "polymorphous perverse". Many students of animal behaviour have noticed parallel phenomena in mammals and birds.

4. In later phases of development (initiated by further maturation, arousal and conditioning processes) low-level instincts unite into larger wholes under the governance ("Primat") of higher level instincts. In these integrative processes the object and goal towards which a higher level instinct will be directed is for a large part built up by the characteristics of the objects and goals towards which the participating lower level instincts are directed owing to their previous development. In other words, translated into ethological terminology, the releasing sign stimulus and the consummatory act of a higher level instinct is for the most part built up by the adoption of the releasing stimuli and consummatory acts of the lower level instincts which compose them, or by a recombination of elements derived from them[1]. The organisation of behaviour is so to speak built up from the bottom, step by step. (See also

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[1] To some extent, however, a reorganisation and reconditioning of the participating lower level instincts may occur. Although these adaptive processes are of greatest importance to the therapeutic practitioner, it would take too long to digress upon them here. (See also Chap. IV, § 2.)

Kuo and Padilla.) Moreover, whether a high level instinct will be aroused or not, may co-depend on the previous development achieved by its subordinate lower level instincts. (E.g. vaginal sexuality in women is aroused as a rule through the intermediacy of clitoris sexuality.) These phenomena, too, find their counterpart in Birch's experiments with "Elizabethan ruffs" and Riess' experiments preventing manipulation in rats (Lehrmann 1953).

5. If in this development the building stones appear not to fit each other or cannot be fitted in under the supremacy of the superordinate instinct, integration will fail and a developmental stagnation of *fixation* will follow. In such cases the controversial drives may continue to lead a more or less independent existence or they may be converted into a neurosis. Two types of fixation may be distinguished: fixation to an infantile object (e. g. a man who marries an elderly woman, i. e. a woman resembling his mother in some respects), and fixation to an infantile level of instinct organisation (e. g. a man who is unable to love the woman with whom he has sexual intercourse or to have sexual intercourse with the woman he loves). In most cases of fixation both types occur together and cannot be sharply distinguished. In animals the first type seems to be the common one, at least judging from imprinting experiments[1]. The second type has been observed in herons as a result of an unintentional experiment which took place at the Amsterdam Zoo. Four herons were kept together in a small cage from about three weeks old until about six months old when they were pinioned and placed in a large enclosure together with some other herons, storks, cormorants and pelicans. During the ensueing years these four herons remained united in a "breeding quartet", probably consisting of three males and one female. They lived in perfect harmony, inhabiting one nest, and raised several chicks. Evidently the enforced relationship in the first six months of life caused them to maintain the type of sexual club-formation often observed in nest-companions before independence is attained (Portielje and Kortlandt, unpublished). Other cases of fixation in animals have been described under the heading of "experimental neurosis" in American literature. (See also Holzapfel, 1939.)

6. From birth to full adulthood, development appears to proceed in an oscillatory course. Periods of progress alternate with static periods ("Latenzzeiten") and this sequence is correlated to the four main levels of instinct organisation mentioned above. Similar alternations have been observed in the development of animal behaviour by

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[1] In ethological terminology "imprinting" indicates both the process itself and its result whereas in psychoanalytical terminology the *process* is called object choosing or object finding and the *result* is called fixation.

Meyer-Holzapfel (1949) and Kortlandt (summarised in Chapters II and IV of this paper). There seems to be a definite relationship between hierarchical organisation and discontinuous development, but the reason why is not quite clear.

Psychoanalysis and the study of animal behaviour

In the conception of hierarchy summarised above, nearly all the problems which students of animal behaviour are painstakingly dealing with, and also many other problems, were amalgamated by Freud some fifty years ago into one comprehensive and coherent scheme of concepts. Such phenomena as object finding, goal finding, priming and hierarchy were considered to be closely interwoven. A student of animal behaviour who ignores all this will find himself in a similar position to an atomic scientist who ignores Einstein's theory of relativity: in such a case ones basic theoretical knowledge is fifty years behind the times.

Of course in this paper only those aspects of psychoanalytical theory which refer to our problem have been included here. With increasing knowledge of animal behaviour, however, we may expect an increase of points of contact between both sciences. Striking examples of this trend are found in the recent development of psychosomatic medicine.

In this connection there is, however, one major difficulty. Psychoanalysis is not a pure but an applied science, mainly interested in therapy. Practitioners as a rule do not worry about such academic questions as to whether their science is an objectivist, subjectivist, or mixed one. Their main concern is how to cure their patients, and their system of scientific ideas is adapted only to this purpose. Therefore it requires a good deal of practical experience in psychoanalytical technique before one is able to translate Freud's concepts into contemporary ethological language. This difficulty can only be overcome by a double training: either by training as a student of behaviour in psychoanalysis or by training as a psychoanalyst in the study of animal behaviour. Neither of these sciences can be learned from books only.

Generally speaking, Freud's psychological theories can be considered to be an objectivist science as far as they are dealing with unconscious processes, for *per definitionem* unconscious phenomena are just the contrary to subjective (i. e. introspective or mental) phenomena. At least Freud has left no doubt that instinctual drives cannot be fruitfully studied by introspection and that his concept of instinct was ultimately intended to be a physiological notion, even if such a physiological notion might have an "as if" quality[1] (Ges. Werke V, p. 118; X, pp. 218-219; Stand. Ed. VII, p. 216). On the other hand, however, the operating of these instinctive forces is assumed to be aroused, modelled and re-modelled by pleasure (German: Lust) which clearly is an introspective concept. FREUD's theories are carried by a dualistic approach towards human nature. Further, the difficulty remains that psychoanalytical knowledge of instincts in man has been largely gained through the use of introspective techniques and therefore this knowledge cannot be transferred just as it stands into objectivist thinking. It is beyond the scope of this paper to follow up this point, as it would also be to enter into a critical examination of the system and number of instincts assumed by FREUD. It may be remarked only that investigations on animal behaviour may sometimes clarify those points in psychoanalytical theory which until now have remained rather obscure, e. g. the relationship between "sex" and "love" (KORTLANDT 1949).

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[1] In this context it must be remembered that Freud was a prominent neurologist for twenty years before founding psychoanalysis. He wrote thirty papers on neurological (see cont. p. 162)

Agreement and disagreement in other fields of research

Fifty years have elapsed since the first edition of the "Drei Abhandlungen zur Sexualtheorie". During this period FREUD's conception has been discussed, tested, reconsidered, revised, contested or rejected from many sides. It has exerted great influence not only in FREUD's followers, including some heretics among them, but also in his opponents. In the first category the psychoanalyst and investigator of ants R. BRUN (1926) may be especially mentioned because he seems to have been the first to use the term: "hierarchy of instincts".

Several points in FREUD's views are still subject to much controversy but on the whole, those features which have been summarised above in points 3, 4 and 6 have found fairly general acceptance, not only among psychotherapeutists but also among those who for the most part reject FREUD's theories. In other words, the idea that in man there exists a hierarchically organised driving system and that this system develops by ascending stages during ontogeny is a current one in present-day psychology, at least on the Continent of Europe. This fairly general acceptance may be attributed to a large extent to the fact that investigations outside the area of psychoanalysis have led to conclusions of a similar kind.

From the neurophysiological side the idea of hierarchy was supported by the then famous Swiss neurologist VON MONAKOW who launched an interesting theory on instinct organisation in which points 3, 4 and 5

(cont. note p. 161)

and allied subjects, and continued to think in neurological concepts throughout his life (SPEHLMANN 1953). Moreover, FREUD was "above all a biologist" as was recently stated by RÜMKE, President of the World Federation for Mental Health, in his commemorative speech at the unveiling of the FREUD memorial in Vienna.

were summarised as the principle of "développement en briques". (Stone-by-stone development, or ascending development, or isolated development followed by ascending integration; see especially VON MONAKOW and MOURGUE 1928.) Ontogenetic development of behaviour was recognised to follow a cyclical or, more precisely, spiral course, in which disintegrative phases lead on to subsequent phases of integration at a new, higher and more comprehensive level than previously attained (MAEDER 1925, RÜMKE 1933).

From the point of view of non-psychoanalytical child psychology, ideas of a similar tenor as points 3, 4 and 5 summarised above, were introduced by CHARLOTTE BÜHLER (1928) in her "Phasenlehre" (the doctrine of development in phases) which was based upon extensive observation work by means of objectivist (i. e. ethological) methods. She found that child development proceeds from performance games (resembling vacuum-activities), via construction games, to task setting behaviour, which process follows an ascending course. Convergent lines of thought were applied in the educational system of MARIA MONTESSORI in which during education the organisation of behaviour is deliberately built up from the bottom, step by step and phase by phase, thereby making use of sensitive periods in order to model the constituent parts in such a way that they would fit together when being integrated later into a whole. Other authors produced analogous ideas (e. g. GESELL 1954). Apparently the notion of ascending development has been a fruitful one.

All these trends of thought state more or less the contrary of the well-known principle of COGHILL: "Behaviour develops from the beginning through the progressive expansion of a perfectly integrated total pattern and the individuation within it of partial patterns which acquire various degrees of discreteness" (COGHILL 1929). In CH. BÜHLER's writings for example, the differentiation of mechanical and logical memory proceeding at the age of twelve years seems to be the only case of a Coghillian type of development described by her. Evidently in Continental Europe the scientific views summarised above found a breeding ground well prepared by the Hegelian philosophy with its slogan "thesis–antithesis–synthesis" and by a political history leading cyclically onward. Further the idea of organisational levels has been a common notion from ARISTOTLE in the past to the philosopher MAX SCHELER (1930), the psychologist ROTHACKER (1941) and the neurologist GOLDSTEIN (1934) in the present. In England on the other hand, with its Darwinian antecedents and its tradition of more gradual social and political evolution, Coghillian ideas could apparently more easily take root.

There have been, however, in Continental scientific thinking, influential counter-trends as well. During the inter-war years the principle of Wholism (Ganzheit) became a dogma that was almost unshakable. Such a climate was not conducive to the idea of "développement en briques". Consequently the developmental psychology of H. Werner (which can be considered to be an extension of the Coghillian principle) gained much influence and considerably hampered and retarded full appreciation of the far reaching bearing of the developmental principles discovered by Freud, von Monakow, Ch. Bühler and others who, along different lines of research, had come to essentially the same conclusions. Nevertheless the idea of ascending development gained adherence.

The present situation in Continental psychology seems to be that most psychotherapeutists and the majority of child psychologists have accepted the essential features of Freud, von Monakow, Ch. Bühler and similar conceptions with regard to ontogenetical development of the organisation of behaviour, even including those psychiatrists and and psychologists who reject many other aspects of psychoanalytical theories. It would be difficult indeed to imagine Continental psychology and psychiatry without the general idea of a hierarchical construction process during ontogeny of the driving forces. In Holland at least, the doctrine according to which psychological development in man proceeds in stages during which independently maturing instincts build up a hierarchical organisation by successive steps of integration, has become a generally accepted item in the curriculum for students of medicine, psychology and social case work. Hierarchy and the principle of ascending development is no longer a theory; it has become a generally recognised fact, at least in modern developmental psychology. It is interesting to realise that this conclusion has been arrived at as a result of objectivist lines of approach and not by introspection. We will return to this point later (pp. 167 and 185).

II. THE IDEA OF HIERACHY IN "HORMIC" AND "DYNAMIC" ANIMAL PSYCHOLOGY

Another trend running through scientific thinking on the hierarchy of instincts starts with Lloyd Morgan, McDougall, Shand and some other English and American authors. This trend will be considered now and it will be seen that although the idea of hierarchy was conceived, the bearing of this principle has not been fully recognised owing to much confusion over the word "instinct" and its subsidiary attributes.

Some of the authors indicated above preferred to use the word "instinct" or "drive" in order to denote the *high* level driving forces in the organisation of instincts (e. g. food-seeking instinct, parental instinct, mating instinct, gregarious instinct, and so on; totalling about twelve or fourteen or even eighteen instincts according to McDOUGALL, 1908, 1923, 1932). Other authors, however, e. g. SHAND, preferred to use the word "instinct" or "drive" to designate the innate motor patterns, i. e. the *lowest* level in the innate organisation of behaviour. Hence the distinction between "major" instincts or drives and "minor" instincts or drives which was introduced and in which the major instincts were supposed to be *driving* agents or propensities and the minor instincts were thought of as *being driven.* In this terminology the word instinct had a twofold meaning, at one time referring to the propelling forces and at the other referring to the innateness of behaviour patterns. At first glance the terms major and minor seem to suggest a hierarchy but this impression would be wrong. In some cases, however, the minor instincts were assumed to be driving agents as well, similar to the so-called Erbkoordinationen described by LORENZ, and in these cases a hierarchy of driving forces was assumed. It was indeed a rather confusing matter.

LLOYD MORGAN'*s conception of hierarchy*

Still more confusion was created when LLOYD MORGAN (1920) made a distinction in instincts of six different levels. At the highest level only two "instincts" were recognised: self-preservation and race-maintenance. It will be clear that at this level the word "instinct" has only a *classificatory* connotation with regard to the biological *functions* or teleological purposes of behaviour and that it does *not* refer to the organisation of driving forces inside the organism.

The second, third and fourth level instincts, taken together as "mid-level instincts" in LLOYD MORGAN's terminology, "are those with which many writers on instinct, Dr. McDOUGALL for example, almost exclusively deal", as it is stated explicitly in LLOYD MORGAN's paper (p. 277). Now, in McDOUGALL's terminology, instinct means driving agent. Hence the word "instinct" in *mid-level instinct* according to LLOYD MORGAN has quite a different connotation from that in *high-level instinct:* for this time it "means a larger instinctive whole within which contributory instincts of a simpler kind are incorporated" or "organised" (loc. cit., p. 273). Evidently LLOYD MORGAN has recognised here a hierarchical organisation of "mid-level instincts" on three levels, and in this context hierarchy of "mid-level instincts" means essentially the same as hierarchy of "instincts" (or centres) according to the concepts of contemporary ethology, in view of the fact that McDOUGALL's concept of instinct implies a propelling force and therefore may be regarded as equivalent to the ethological concept of instinct, or centre, at least as far as hierarchy in the driving system is concerned[1].

An interesting point is that LLOYD MORGAN illustrates his argument with a description of bird behaviour taken from HOWARD in which LLOYD MORGAN (perhaps without sufficient grounds) thought to find a description of the actual driving system. LLOYD MORGAN therefore seems to have been the first to recognise hierarchical organisation of instincts in animals other than man, but he did not take the trouble (or had no means available) to prove his thesis by means of detailed analytical research.

The "fifth level instincts" according to LLOYD MORGAN's enumeration are "the primitive instinctive responses as normally elicited by adequate stimulation". Evidently in this category of instincts no endogenous reaction-specific stimulus generation (as it would be called in contemporary ethological terminology) is postulated, which makes a difference from the "mid-level instincts" which do generate drives. For the rest, the "fifth-level instincts" are supposed to be subordinate to and driven by the fourth level instincts. Hence the "fifth-level instincts" are identical to McDOUGALL's concept of "motor mechanisms": tools in the hands of the driving instincts. (Cf. Fig. 9b, p. 213.)

Finally the sixth level in the scheme consists of the reflexes which are supposed to combine in the "primitive instinctive responses" but with regard to which LLOYD MORGAN states that "nothing need here be said" and for the rest refers to SHERRINGTON's works.

It appears that LLOYD MORGAN's ideas on hierarchy have met with little response. This may be partly due to the confusion which was aroused as a consequence of his use of the word "instinct" in three or even four different connotations. The results of this confusion persisted for a long time. (See HOLMES 1922; BIERENS DE HAAN 1940, pp. 81–88.) Further, the lack of analytical interest among animal psychologists at that time was not conducive to specific research on hierarchy and, moreover, the then prevailing opinions on decency seriously hampered the introduction of psychoanalytical concepts on hierarchy into general psychology and animal psychology.

McDOUGALL's *linkage of instinct with emotion*

There seems to be, however, a still further reason. In McDOUGALL's books one can find quite a large number of hesitations and contradictions especially on this point, but ultimately he always rejected the idea of hierarchy. One gets the impression that this rejection is essentially due to a typical feature in McDOUGALL's definition of "instinct", viz.

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[1] Both concepts imply endogenous generation of motor impulses which in different situations may be discharged by different motor mechanisms. For the rest there are many divergences between these concepts.

the linkage of the objectivist concept of "instinct" with the subjectivist concept of "emotion" in his theories[1]. As a matter of fact, objectivist observation of behaviour very soon reveals the existence of a hierarchical driving system. For example, everybody knows that a satiated dog may hunt as does a hungry dog (which fact McDougall knew too, as we shall see below). This circumstance suggests the existence of a hunting instinct hierarchically subordinate to the food-seeking instinct.

In introspective psychology, however, the state of affairs is quite different: everybody knows what it means to be hungry, but nobody has ever heard of a specific "hunting emotion" in the strict sense of McDougall's primary emotions; or at least it would be very difficult to detect the introspective emotional correlate of such a lower level drive. Apparently there exists no specific link between instincts and emotions: *instincts are hierarchically organised, emotions are not.* In everyday life all activities which are driven by instincts lower than top-level are called "play" or "games", thereby indicating that the major emotions are lacking. It seems therefore that (at least in man) the functioning of lower level instincts as a rule are *not* accompanied by instinct-specific emotions as defined by McDougall[2] and this may be the main reason why McDougall, in spite of obvious behavioural evidence, ultimately insisted on denying the existence of instincts lower than top-level, thereby at the same time denying the existence of a hierarchical organisation of instincts. Instead of this, the hunting behaviour of satiated animals was interpreted as "play" and ascribed to an unspecific surplus of nervous energy according to the theory of Spencer. (McDougall 1923, pp. 171 and 219.) At the cross-roads between objectivist and subjectivist criteria McDougall ultimately chose subjectivism, and therefore failed to recognise hierarchy.

When leaving out of consideration classificatory intended groupings of instincts according to functional or teleological points of view, it seems that Groos (1930, pp. 38–42) and Portielje (1938, pp. 219–220) were the first animal psychologists of the McDougall school who, after Lloyd Morgan, reintroduced the notion of hierarchy, conceived as a hierarchy in the organisation of driving forces in the animal. Both authors, however, remained too much addicted to the McDougall linking of the objectivist conception of "instinct" and the subjectivist conception of "emotion" and in consequence their ideas on hierarchy have never been worked out in a clear-cut form. In Portielje's book and other writings the false hunting of satiated predatory animals and similar activities have been ascribed both to a subordinate hunting drive and to a general surplus of energy without making a definite choice in favour of one of these two explanations.

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[1] According to McDougall's definitions an instinct (or propensity) is a psychophysical disposition inducing at the same time a specific purposive activity and a specific emotional excitement.

[2] According to his definition, pleasure and pain (German: Lust and Unlust) are not primary emotions but accessory phenomena.

Portielje's *concept of differentiation*

Portielje has, however, paved the way for the concept of hierarchy in a different manner. From 1927 onward, all his papers give consideration to the so-called "differentiation" of drives and emotions (drives and moods in ethological terminology). According to his view, ontogeny and seasonal maturation in animals are differentiation processes during which the objects, goals and emotional qualities are at first rather vague and undetermined but gradually become more and more definite, diverse, clear-cut and purposive. Further, apart from maturation, at a given moment a drive or urge may be now more now less differentiated. In this way the word differentiation is used in another connotation than by McDougall who uses it only to indicate the splitting up of one instinct into two instincts in the course of phylogeny.

It will be clear that these ideas suggest a hierarchy of generalised, respectively specialised, internal states (emotions or moods) in the animal, as was conceived in later years by Baerends and Tinbergen. (See Chap. III.) As a description of actual behaviour, Portielje's term "undifferentiated emotion" can be considered to be almost a synonym for "high level mood" in ethological terminology. In this respect it was Portielje who pointed the way to the ideas on hierarchy which have subsequently been devised by his countrymen.

Another feature is that Portielje's ideas show a clear relationship to those of Coghill discussed above because both writers assume a gradual differentiation in the course of ontogeny. On the other hand, Portielje's conception is, at the same time, reminiscent of the views of Freud, von Monakow, Ch. Bühler, etc., in so far as the term differentiation implies both an increase of selectivity with regard to the releasing situation and an increase in purposiveness with regard to the mode of behaviour during ontogenetical development. There is, nevertheless, a divergence between these writers: whereas according to Freud, von Monakow, and Ch. Bühler these ontogenetical processes follow mainly an additive and integrative course, according to Portielje their course is mainly differentiative. For the rest von Monakow's principle of "développement en briques" is recognised by Portielje as well under the term "integration", but in his account it is estimated to be of less importance than differentiation.

In Chapter I we have seen that emphasis on the differentiative type of development is not conducive to the discovery of hierarchy, for reasons expounded there. Anticipating what will be said further on in this Chapter we may say here that a differentiative type of development during ontogeny *does not* as a rule lead to a hierarchical type of instinct organisation, whereas an integrative type of development as a rule *does*. Therefore it would seem that PORTIELJE's emphasis on differentiation and wholeness, as well as his attachment to the McDOUGALL linking may have prevented his recognising the full implications of the principle of hierarchy. For the rest it remains to his credit that he drew the attention of his countrymen to these problems and also that he was the first writer after BRUN who tried to bridge the gap between medical and animal psychology. The fruitfulness of the latter point will be considered later on in this paper.

Hierarchy of "appetites" as defined by KORTLANDT *in 1940*

Enlarging on PORTIELJE's findings, his pupil KORTLANDT (1940 a, b and c) found evidence of a complicated hierarchical organisation in the behaviour of European cormorants. In his account the term "instinct" was avoided because it was so confusing. Two hierarchical systems were distinguished: a driving hierarchy of so-called "appetites" (needs or wants, German: Bedürfnisse) and a discharging hierarchy of "propensity dispositions" (German: Triebdispositionen). Moreover, parallel to the first system a system of "emotions" (Affekte) was postulated, and these emotions were assumed to be subjective correlates of activated appetites. In other words, appetites and propensity dispositions must be taken as objectivist concepts designating two different kinds of instincts or behaviour mechanisms, whereas emotions must be taken as subjectivist concepts indicating the "inner" or "mental" state of the animal. With regard to the propensity dispositions *no* subjective correlates accompanying activation were assumed.

In this peculiar dualistic conception the McDOUGALL link between instinct and emotion was maintained as far as appetites were concerned but rejected as far as propensity dispositions were concerned. Further, in contrast to McDOUGALL, when at the cross-roads between objectivist and subjectivist animal psychology, KORTLANDT attached primary importance to objectivist criteria. He thus recognised hierarchy and consequently was compelled to assume a corresponding hierarchical system of emotions although as a matter of fact in introspective human psychology no evidence can be found in favour of such a hierarchy of primary emotions. As a further consequence, emotion was redefined in such a way that it could be conceived also as an objectivist concept, viz. as a co-ordinating force.

In the writer's opinion to date, the *theoretical* considerations expressed in his papers of 1940 and summarised above were a fallacy. The observational facts, however, remain unaffected and may be inserted in a revised theoretical setting in which the McDougall link would be cut through and in which the concept of emotion will be left out of account. In the present paper the hierarchy of appetites will be dealt with because it may be considered to be, so to speak, "true hierarchy" whereas the system of propensity dispositions may be called a "false hierarchy".

Inference of hierarchy from ontogeny and maturation

Considering that the original papers were published partly in Dutch and partly in German, it seems justifiable to introduce the subject with a translation of some passages quoted from Kortlandt (1940 a, pp. 389–393) in which the essential observational facts are given. To commence with, a definition will be given and then the quotation will proceed with a description of cormorant behaviour.

"If we observe that an animal is striving towards a goal and in doing so demonstrates in its behaviour an adaptive variability in such a way that the variations serve a purpose, then we are sure that we are dealing with the expression of an appetite which needs satisfaction[1].

The first system of appetites to be considered in the cormorant is nesting. Why does a cormorant build a nest? A simple question but not so simple to answer.

In consequence of spontaneous maturation, ontogenetical development of nest-building proceeds as follows: At an age of 2 weeks the young bird now and then (but still only rarely) performs the so-called twig-quivering with a twig held in the bill. As the bird gets older this movement, a very characteristic trembling movement, is performed more and more often, and, at the age of 5 weeks, a new element appears: while twig-quivering, the young bird will make jabbing and pressing movements, sideways and downwards, which it *continues to do until* the twig gets fastened in the nest.[2] The bird is very persistent until the twig is firmly fixed. At a still later age, the young birds collect twigs while walking and climbing in the vicinity in order to insert them in their own nest[3], or they do the same with twigs which are brought to the nest and handed over by their male parent. So now we understand the biological meaning of twig-quivering: it is owing to these little jabs and pulls that the twigs become entangled in the material of which the nest consists and are thus caught in more securely.

At the beginning of this development the young bird is not interested in the outcome of its twig-quivering. It quivers only at random, so to speak, or, to be more precise, at that age twig-quivering is not yet directed towards a goal; it is a goal in itself and an expression of the quivering appetite as such. From an age of 5 weeks and onwards, however, the twig-quivering is used as a means towards a goal, viz. to fasten twigs into the nest. If after longer or shorter working the twig sticks fast then the goal is attained and the appetite for fastened twigs is satisfied. (*Addition 1954:* in other words, quivering and jabbing then cease.) When nesting, a cormorant cannot bear a twig to be loose and if necessary it will pull the loose twig out of the nest and put it back again more firmly by industriously quivering. In doing so, it satisfies not only the appetite for the twigs being fastened in its nest but it also satisfies the quivering appetite, which was revealed in the immature behaviour of the bird of 2 weeks old. Thus we here discover two appetites, the one so to speak included in the other, for the pursuit of the goal of higher order (i. e. the fastened twig) is done by achieving the goal of lower order (i. e. quivering as a purpose in itself). This phenomenon I would chose to call "concentric purposivenesses" considering that twig-quivering is a less comprehensive purpose, whereas the twig being firmly fastened is a more comprehensive purpose, or a purpose of higher order[1].

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[1] *Annotation 1954:* Elsewhere in the original paper (pp. 389, 393, 397) it was laid down that the goal by which satisfaction can be attained may be either a consummatory act or a consummatory situation, according to the nature of the particular appetite.

[2] *Addition 1954:* According to data which have been worked out since then, the age at which this behaviour appears ranges normally from 4 to 5 weeks. (In one individual case 16 days, in another case 25 days.)

[3] *Addition 1954:* The age at which this more elaborate building behaviour develops is about 6 or 7 weeks.

This distinction can be extended still further. When commencing reproduction a cormorant will try to acquire a nest in various ways, e. g. by building one, and also by other means. This is always done in such a manner that the means chosen appropriately serve their purpose. The facts are as follows:

In spring many cormorant males take possession of an old nest and then seek to attract a female. During pair formation and for some time afterwards, these males bring nesting material and repair their nests. When all old nests have been claimed and still more males arrive in the colony, there is sometimes fierce fighting for the possession of a nest. Evidently, in males, the appetite for owning a nest is active soon after their arrival in the breeding colony. Those males for whom old nests are no longer available will settle in the crutch of a branch and there solicit for a female. The females ready to mate show a distinct preference for the most active male in sexual and nesting behaviour, irrespective of whether he owns a nest or is settled in the fork of a branch. This indicates that at this time the females have not yet developed an appetite for owning a nest.

If the female courts, accepts and finally "marries" a male in a forked branch, the male will bring nesting material and together they will try to build a nest. Such males will bring much more nesting material than those which have occupied an old nest. Evidently the *appetite for owning a nest impels the male* to greater nesting activity.[2] Often, however, building operations fail because the chosen forked branch is unsuitable. In some cases such a pair will try to raid and capture a neighbouring nest, which may lead to a general fight with all the nestless birds joining in. Further, if building continues to fail, the female eventually will also collect nesting material, thus giving evidence of having acquired an appetite for owning a nest. Moreover she becomes less faithful to her mate and finally, when she is about to lay, she will leave him and pair with another male, viz. a male that does own a nest. She therefore "marries" for a home and not for a husband!

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[1] *Annotation 1954:* In his unpublished notes written before 1940 the present writer actually did use the term "hierarchy", possibly on PORTIELJE's suggestion. In 1940, however, being unaware that this term had already been used by R. BRUN, he decided to abandon the term "hierarchy" and to introduce the term "concentricity" instead of it, in order to indicate that a minor system is incorporated or organised within a major system, and a minor goal within a major goal, and also in order to avoid more definite implications. At this present time, however, the rather awkward expression "concentric purposiveness" should be dropped and replaced by "hierarchical appetites", or hierarchically organised appetites.

[2] *Addition 1954:* This appetite is assumed to be directed towards a consummatory situation and not towards a consummatory act.

Thus far we have found that the male, from his return to the colony onwards, tries by various means to obtain the possession of a nest; but this does not apply to the female until she becomes broody. (*Addition 1954:* After the completion of the nest there is a marked drop in building activities and building is only resumed if the nest proves faulty owing to decay.)

It appears, therefore, that both sexes may use purposive fastening of twigs as a means to a goal of still higher order, viz. to obtain a nest and thereby satisfy the appetite for owning a nest. At an earlier age the goals of twig-quivering were the quivering movement in itself and the twig being firmly fastened; but now the goal of fastening twigs is, at the same time, to own a nest. Hence, by pursuing the goal of the highest order, the two goals of lower order are attained at the same time. To summarise, we may conclude that the ontogeny of the nesting behaviour system in the cormorant reveals three concentric purposive systems. The possibility of this analysis is due to the fortunate circumstance that the different concentric purposive systems mature successively."

At this point the quotation may be interrupted in order to review the factual contents of the statements that have been made. It will be clear that the type of behaviour organisation described above is essentially an organisation of *goals* or *purposes* towards which the animal is assumed to strive. There is nothing mysterious about this. A "goal" is either the performance of a specific activity (consummatory act) or the presence of a specific external object or situation (consummatory situation) which *causes the ending* of a *variable* sequence or series of activities (instrumental acts, or appetitive behaviour) *leading to* this particular activity or situation. No subjectivist or vitalistic implications are made[1]. It appears that these goals are arranged in three levels that successively mature and integrate during ontogeny and seasonal maturation according to the principles described by FREUD, VON MONAKOW and BÜHLER, and further it appears that the pursuit and attainment of a lower level goal may or may not be used as a means to an end in order to attain a higher level goal towards which the animal is striving. In other words, one and the same activity may at the same time function as a consummatory act (at its own level) and as an instrumental act (at its next higher level).

Two aspects of hierarchical arrangement

Of course, levels do not yet imply the existence of a true hierarchy, for in common speech the notion of hierarchy presupposes a *branched* system. This feature is considered more in detail in the following further analysis quoted from KORTLANDT 1940 a (pp. 393–394).

[1] It is often argued that, from an objectivist point of view, a "goal" cannot be a "cause" and therefore cannot be taken into consideration in an objectivist science. This opinion is fallacious. A goal *is* a "cause" indeed, not of a beginning but of an ending. In this strict sense a goal determines the preceding: it determines the continuation of a process.

"In many cases the appetite of higher order can be aberrantly satisfied by means of an experiment made in such a way that, at the same time, the satisfaction of the lower order appetite is prevented and in consequence continues to manifest its effect on behaviour. There is no need to do this in a laboratory; nature may be said to experiment as well. If, for example, a pair of cormorants settle down at an old nest which is still in a good state, then the highest order appetite (i. e. the appetite for owning a nest) is satisfied without any nest-building. Nevertheless in that case the male still appears to bring and fasten (or to have it fastened by his female) quite a lot of nesting material, although it is only a little quantity compared to what is brought by a nestless male. As a rule these twigs are handed over to the female and fastened by her. If, however, she momentarily "has no mind" to do so, then the male will do it himself, thereby indicating that at that moment his goal is *not fastening*, *nor handing over*, but that the twig shall be fastened in tight. So the question is, since everything was firmly fastened before he flew away, why did he bring a twig? There is no other possibility than to postulate yet a fourth appetite, viz. the appetite for bringing twigs. This appetite occurs practically only in the male cormorant. Thus the four appetites with regard to nesting are: the appetite to quiver, the appetite for fastened twigs, the appetite to bring twigs, and the appetite to own a nest. (*Addition 1954:* Bringing twigs cannot be considered appetitive behaviour serving to release quivering, for a cormorant in a specific quivering mood will quiver as well with twigs that are firmly stuck. Moreover, the bringing is done as a rule by the male and the inserting by the female.)

Further, of course, the bringing of a twig is not a means to ensure that the twigs should stick tight and in this respect it differs from quivering. Therefore we do not find here two appetites (goals) one of which embraces the other, but two appetites (goals) which are arranged beside each other as indicated in Fig. 1.

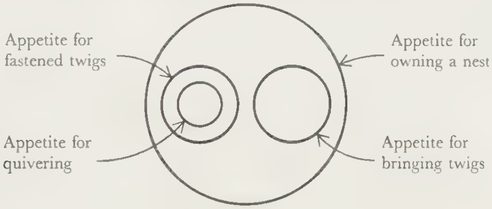
Appetite for fastened twigs
Appetite for owning a nest
Appetite for quivering
Appetite for bringing twigs

Fig. 1

Some comments and conclusions

Thus far the original paper has been followed, apart from some minor abridgements, but today Fig. 1 would of course be drawn in another way, viz. as represented in Fig. 2. However, from the point of view of neural localisation there seems to be no special reason to suppose that Fig. 2 would be more appropriate than Fig. 1, because we do not know the nature of the neurophysiological basis of hierarchy. One might imagine the possibility that the hierarchy of appetites is based upon a hierarchy of hormones or other differentiated physiological conditions rather than upon a hierarchy of nervous centres.

It will be clear that the hierarchy which has been drawn in Figs. 1 and 2 represents only a hierarchy of appetites, i. e. essentially a hierarchy of *goals* (or consummatory acts and situations) towards which the animal appears to strive by means of different and variable forms of appetitive behaviour (as it would be called in contemporary ethological terminology). In other words, it is *not* intended that these Figs. should represent a hierarchy of appetitive behaviour *patterns*. For this reason the attempts at robbing ("raids") which are made by nestless cormorants in order to acquire a nest have not been inserted in the diagrams, as it is assumed that in the cormorant there is no evidence for the existence of a special sub-appetite for raiding inhabited nests. Raiding is only a tool, a means to an end, an instrumental act, not a goal in itself. It is only appetitive behaviour. The same applies to other aggressive ways of acquiring a nest. Twig-quivering and bringing twigs on the other hand are consummatory acts in themselves as well as instrumental acts (i. e. appetitive behaviour) towards a higher level goal, and therefore the appetites corresponding to them have been inserted.

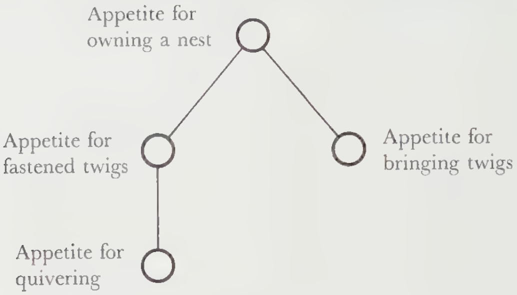
Appetite for owning a nest
Appetite for fastened twigs
Appetite for bringing twigs
Appetite for quivering

Fig. 2

For some purposes it might be clearer if appetites as well as motor mechanisms serving the satisfaction of them could be represented in one diagram, and this might be done by indicating such a motor mechanism by a small dot. In this way, according to the description quoted above, the following scheme of nesting behaviour in the male cormorant is obtained: (Fig. 3)

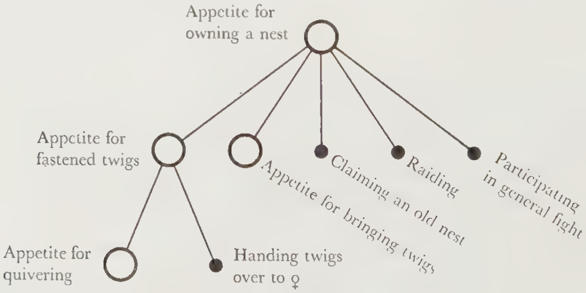
Appetite for owning a nest
Appetite for fastened twigs
Appetite for bringing twigs
Claiming an old nest
Raiding
Participating in general fight
Appetite for quivering
Handing twigs over to ♀

Fig. 3. The nesting system in the male cormorant

With regard to the female cormorant the picture is somewhat different. As indicated above, the female becomes interested in the presence of a nest not earlier than when she becomes broody, i. e. when false-incubating starts. Before that time, if there is no nest, she will neither bring twigs nor change her mate for a nest-owning male[1]. Moreover, after the young have fledged or prematurely left their nest by climbing or walking, territorial defence on the part of the female will cease whereas the male will continue it. Evidently in the female there exists *no independent or autonomous* appetite for owning a nest. Her acting and striving towards the possession of a nest is only appetitive behaviour subordinate to the appetite for incubating eggs and caring for chicks, i. e. parental behaviour. She does, however, insert and quiver twigs during the preliminary period when she is still uninterested in the presence or absence of a nest, just as she did when she was 5 weeks old. Therefore in the mature female the scheme can be drawn as follows: (Fig. 4)

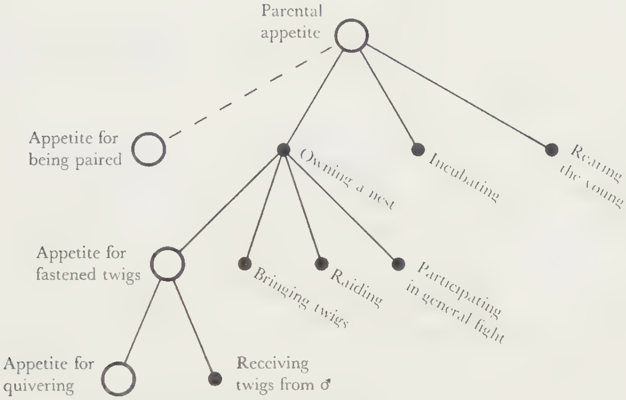

Fig. 4. The parental system in the female cormorant

In the male, on the other hand, there seems to exist no special connection between the parental appetite and the appetite for owning a nest: both appetites are top-level ones and the appetite for a nest is not subordinate to the parental appetite.

Following this way of reasoning, according to the papers of 1940, the top-level appetites with regard to reproduction as recognised in the mature cormorant were:

In the male: the appetite for owning a nest, the appetite for being paired, the appetite for cloacal contact, the appetite to incubate and the appetite for the care of the young.

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[1] Except in special cases which are not to the point here.

In the female: the same, except for the appetite for owning a nest.

(Annotation 1954:) At the present time this picture can be largely maintained. There are still no reasons to postulate a "reproductive appetite", i. e. a reproductive instinct as postulated by some recent authors; or, if such an instinct occurs, it can be attributed exclusively to the female. Further, we must assume that in the female the appetite for being paired becomes integrated under the control of the parental appetite and thereby loses its autonomy or independence as soon as, in the course of the breeding cycle, the parental appetite comes into action. Thus the female represents a more centralised type of organisation than the male. In *bisexual* females the bringing of twigs should be represented by a circle instead of a dot in Fig. 4. Finally we must assume that in males and females, incubating and rearing the young are not expressions of different appetites but represent phases, or sets, or "garnitures" (Kortlandt, 1949) belonging to one single parental appetite.

Further consideration of ontogeny

After this digression we will return to the original paper in order to study in more detail the ontogeny of nesting behaviour (1940a, pp. 398–399, abridged).

> "On attaining the age of one year, cormorants as a rule return to the colony in April or May. They then show some appetite for a nest, but as nearly all the nests are occupied by breeding pairs or young, the one year old birds are thus forced to attempt raids on nests containing young birds whose parents are absent. If the attempt is successful the chicks will be thrown out and the raider will spend some time at the nest, and will then fly away satisfied.
>
> Probably these raiders are all males. Only very exceptionally do they perform nesting activities (i. e. bringing or inserting twigs, or quivering). The question now is: why do these nest wanting birds not start building a nest, since they are able to build? Here we find a case in which an animal *is unable to use an activity for the higher order purpose* which it is intended to serve, although this activity is potentially present in the animal." (*Annotation 1954:* The potential presence of the activity was assumed because when about two months old the young cormorant did build, insert and quiver; and, moreover, when one year old, displacement-quivering still occurs. In the original paper a

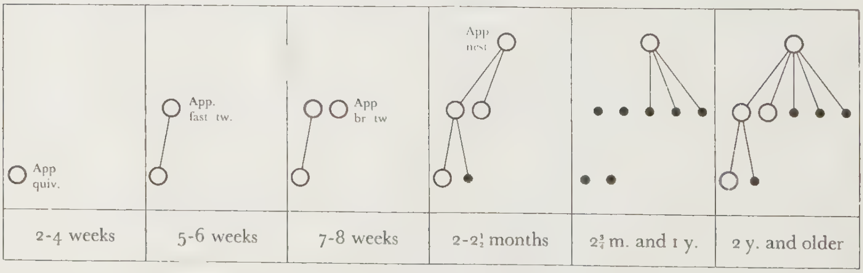


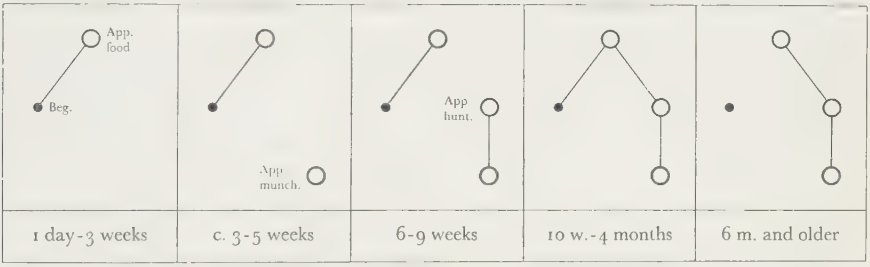
Fig. 5. Ontogeny and maturation of male nesting behaviour

tentative explanation of these phenomena was given, but this explanation cannot now be maintained and may therefore be omitted here. See also Chap. IV, § 4, p. 260.)

The findings with regard to the ontogeny of male nesting behaviour as given in these quotations can be rendered now schematically in a series of diagrams: (Fig. 5)

It must be emphasised that this scheme applies especially to males. In one-year-old females there is some evidence suggesting that the top-level appetite of nesting behaviour is already represented by the parental appetite, as may be inferred from false-incubating. Consequently in these females the appetite for a nest should be indicated by a dot instead of a circle.

A similar type of ascending development was described in food-seeking behaviour, sexual behaviour, pair-forming behaviour (not to be confused with sexual behaviour!), parental behaviour, and also partly in the later development of fighting and threat behaviour[1]. (See also Kortlandt, 1940 b.) For example, food-seeking develops as indicated in Fig. 6. In this context it is an important point that the appetite for hunting and the appetite for munching fish can be kept largely unsatisfied by putting cormorants in a zoo and feeding them on dead fish. Then for the rest of their lives these birds will continue to perform false-hunting and false-munching on twigs and litter in just the same way as young cormorants do up to the age at which the connection between the appetite for food and the appetite for hunting matures (1940 a, p. 396). In nature, on the other hand, after maturation of this connection, these sub-appetites are always satisfied in the course of normal food-seeking. In other words the existence of a sub-appetite is discovered by setting up an experimental situation in which this sub-appetite remains unsatisfied. The principle is the same as explained above with regard to the influence on building behaviour exerted by



1 day-3 weeks | c. 3-5 weeks | 6-9 weeks | 10 w.-4 months | 6 m. and older

Fig. 6. Ontogeny of food-seeking behaviour

the presence or absence of a nest: If a superordinate appetite is satisfied in such a way that the accessory subordinate appetites are *not* also satisfied, the latter will remain to seek their own satisfaction[1].

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[1] The early development of fighting and defence follows another course which will be discussed later on in this paper (p. 183).

Another aspect of the same principle was stated as follows (1940 c, p. 464–465):

"If a particular activity is performed and its instinctive goal is attained, the 'threshold' (Schwelle, LORENZ) will be lowered, not only for this particular activity but also (in a lesser degree) for those activities which are directed towards the same or about the same goal. This phenomenon is very conspicuous in reproductive activities in the cormorant. Hence there exists not only a reaction-specific threshold-lowering but also a similar phenomenon affecting groups of activities. For the rest I prefer to use the term appetites instead of postulating purely hypothetical stimulus-generating substances." Translated into ethological terminology this statement means that not only reaction-specific energies (SAP's, to quote THORPE) were distinguished, but also energies which can be discharged by *any* activity of a definite *group* of activities. ("Group-specific" energies.)

The explanations given above will suffice to make clear the general principle of hierarchy as recognised in the cormorant. It would be impossible here to discuss the hierarchical organisation of pair-forming behaviour which is a very complicated one and in which no less than four levels of appetites were distinguished. It may be mentioned only that the complications of this system are heightened by the fact that the appetite for being paired and the appetite for cloacal contact largely make use of the same behaviour patterns serving as appetitive behaviour (instrumental acts) in order to attain their different goals.

The convergence of findings in cormorant and man

It will be evident that the general tenor of the findings reviewed above with regard to hierarchy and its ontogeny in the cormorant, largely coincides with the principles laid down by FREUD, VON MONAKOW, CH. BÜHLER, and others. At that time (1940) the writer was still largely ignorant of psychoanalytical and other theories and therefore only an allusion was made concerning the similarity in nature of these phenomena in the cormorant and in man, without making a definite statement (1940 a, p. 396). In later papers, however, dealing with the integration of nesting, pair-forming and sexual behaviour, no doubt remained that these phenomena in the cormorant must be considered identical with those in man described by FREUD, and VON MONAKOW and MOURGUE (KORTLANDT 1942, pp. 181, 233, 234, 241, 253, 277, 280; and 1943, pp. 21, 33, 34). But even in 1940 the conclusion was drawn that "the ontogenetic development of behaviour-systems proves in six cases out of seven to be just the reverse of the biogenetic principle of HAECKEL" (1940 b, p. 442).

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[1] The same principle appears to have been recognised and explained already by HECK (1930, p. 93) when describing vacuum-plucking of leaves in giraffes.

The last-mentioned passage may have been the origin of TINBERGEN's erroneous statement: "KORTLANDT emphasizes the fact that the growth of behaviour patterns in the young usually begins with the specialized stereotyped components at or near the end of a chain and that the introductory elements, comprising the appetitive behaviour, are added retrogressively, i. e. in the reverse order to that of their final performance, as in the nesting behaviour. Maturation in the adult is, according to KORTLANDT, 'just the reverse', the generalized appetitive behaviour being performed first, and then the reaction is completed by extension towards the more specialized, subordinated appetitive behaviour until the pattern is completed by the appearance of the consummatory act." (TINBERGEN 1951, pp. 140–141). As a matter of fact this rendering shows no resemblance to any statement ever made by the present writer. To be sure, in all behaviour patterns in the cormorant where a comparison could be drawn, no essential difference between the course of ontogeny and of seasonal maturation has been found. This also applies to intermediate stages which have not been shown in Fig. 5 and similar cases.

In this connection one should not forget that it is entirely impossible to make any statement as to whether "the" appetitive behaviour or "the" consummatory act matures first. The point is that at first *one* consummatory act matures, and then *another one* matures which employs the first one as appetitive behaviour towards the new goal, or that afterwards a *new appetite* matures which is not directed towards an act at all but which employs the so-called "consummatory" act as appetitive behaviour in order to accomplish a situation which has newly become a consummatory one. In LORENZ' film of the grey lag goose one is able to see that the same principle applies to nesting behaviour in this species. For the rest it may be stressed that "dis-maturation" (i. e. when the season is over, or in case of ill-health or psychotraumatic disintegration) proceeds along exactly the same line but in the reverse direction. This fact proves that we are dealing with maturation and "dismaturation" processes and definitely not with learning processes. The course of "dismaturation" therefore affirms the validity of the supposed relation between the degree of maturity and the degree of integration in behaviour.

Selectivity to sign stimuli which release satisfaction

In another respect also the conclusions on hierarchy reached concerning the cormorant appeared to coincide with those obtained on man, viz. with regard to what is called the cognition in McDOUGALL's terminology, or the releasing sign stimulus (or pattern) in ethological language. In order to explain this point we may start again with a quotation (KORTLANDT 1940a, p. 396):

"A nestling cormorant performs fish-munching movements on small twigs, pieces of wood, etc. When about 7 weeks old (after leaving the nest) it will begin to hunt and capture, or more precisely speaking, false-hunt and false-capture, slender oblong objects found in the water. Gradually it will become increasingly selective in its preferences and will restrict itself to objects which closely resemble fish, and finally it will become self-supporting by capturing live fish. Thus maturation of the connection with the superordinate appetite (i. e. hunger) is correlated to an increasing selectivity when choosing the object (Cf. Fig. 6). This is *not* a conditioning process but a case of spontaneous maturation of the innate cognition, for, if we satisfy the superordinate appetite in the fully grown bird by unnatural means, e. g. by feeding a zoo cormorant on dead fish, the subordinate appetite comes to light again and the cormorant will again hunt and capture pieces of wood, straw, string and paper, just as in its youth[1]. This not only

[1] *Annotation 1954:* This phenomenon might be called a *non-neurotic* regression.

> proves that there exists an appetite for hunting apart from the appetite for food, but also that the increasing selectivity of the cognition of the object to be hunted during ontogenetical development has to be attributed to maturation of the connection with the superordinate appetite, viz. the hunger which can be satisfied only by fish."
>
> A similar course of development during ontogeny and seasonal maturation was described in sexual and pair-forming behaviour: at first these activities appear to be vacuum-activities, thereafter they become a form of friendly (perhaps social) greeting, then they become erotic expressions irrespective of the sex and number of the "mates", and finally they are directed only to one member of the opposite sex (1940 a, pp. 395 and 397–398; 1940 b, pp. 429, 430 and 432). For the rest, the same type of development has been found in other birds as well, e. g. in the Hobby Falcon (L. TINBERGEN 1935; SCHUYL, TINBERGEN and TINBERGEN 1936), and in the Common Tern (N. TINBERGEN 1938). The relationship of these facts to hierarchy, however, has not been recognised previously.

In other words, it was assumed that in a hierarchical system each appetite (or "instinct") at any level has its own innate releasing mechanism (IRM) by which the activities satisfying that particular appetite are released, and further, it was assumed that the *bottom*-level appetite has the *least* selective IRM (fish-munching can be released by a chunk of wood), whereas the *middle*-level appetite has a *moderately* selective IRM (false-hunting and capturing require oblong and slender objects), and the *top*-level appetite has the *most* selective IRM (only fish or fish-like objects of soft texture will be swallowed). In addition to this it was postulated that the gradual shift in selectivity observed during ontogeny (from piece of wood to real fish) must be attributed to a gradual shift in the level from which the main body of the motivation originates. (At first mainly from the bottom-level appetite, ultimately mainly from the top-level appetite; see Fig. 6.) Or, more briefly: the higher the level of the drive, the higher the specificity of the goal and the higher the specificity of the stimulus required for releasing the consummatory act or for releasing the actions leading to the consummatory situation.

This is the new setting given by KORTLANDT to PORTIELJE's concept of "differentiation"[1]. Thus, following PORTIELJE and mostly unaware of similar phenomena disclosed by FREUD, hierarchy was stated to be the very core of instinct, the general principle governing the integration of behaviour in ontogeny and maturation, its canalisation in normal functioning, and its disintegration in cases of disturbance, ill-health or seasonal "dismaturation."

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[1] It will be remembered, however, that PORTIELJE's term differentiation is a collective notion under which other phenomena of a different nature are included as well. With regard to the phenomena with which we are dealing at present the term integration is more appropriate than differentiation.

Some miscellaneous points

Additional suggestions were made with regard to the far-reaching importance of this principle. The resemblance in appearance between displacement-activities and immature activities was explained by assuming that both are driven by bottom-level drives (1940 a, pp. 390, 395, 396; 1940 c, p. 499). The difference in appearance between, on the one hand, low-intensity activities (including intention movements) in mature animals and, on the other hand, immature activities as normally shown by immature animals, was attributed to a difference in level of the appetites which originate the drive (1940 a, pp. 397–398; 1940 b, p. 429; 1940 c, pp. 496, 497, 516).[1] The special nature of the activities which are due to the damming up of the drive and threshold-lowering was considered (1940 c, p. 455). The concept of "abreacting" (German: abreagieren, in every-day language: discharging the drive without satisfying the appetite) was tentatively redefined as "achieving a balance between incomplete satisfaction of the top-level appetite and surfeiting of the subordinate appetite" (1940 a, pp. 397 and 400). "Play" was interpreted as a low-level activity of a special nature (1943, pp. 33–34).

From all this it will be apparent that hierarchy (or "concentricity" as it was called at that time) was judged to be a very important principle indeed. It was also judged, however, that there was more in the heaven and earth of animal behaviour than the philosophy of hierarchy alone. Therefore some points will have to be considered now in which other principles than hierarchy play a role.

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[1] In literature the two types of activities mentioned here are often confused or put on an equal footing. (For example in TINBERGEN 1951, p. 141, although TINBERGEN 1940, pp. 32–34, does distinguish them. BAERENDS and BAERENDS-VAN ROON 1950, p. 212, hesitate as to whether a distinction is justified.) There are, however, marked differences between both types. Low-intensity activities ("incipient movements", "intention movements", etc.) when originating from a mature drive are characterised by the rigidity and stereotypedness often ascribed to fixed patterns in general, by a high degree of integration, and by a high degree of selectivity to releasing objects. Immature activities ("awakening activities", but also activities in the "dismaturation" period, "cyclic vestigial activities" ARMSTRONG 1949) are characterised on the contrary by a lack of rigidity and stereotypedness in the fixed patterns, by a low degree of integration and by a low degree of selectivity. This applies not only to cormorants but also to other animals and man. Especially in copulatory behaviour of birds and mammals the phenomenon is very conspicuous. For example, contrary to popular belief, sex offenders in man (and also in cormorants) are suffering as a rule from hyposexuality, rarely from hypersexuality. This fact has also been recognised in hormone therapy (GOLDZIEHER and GOLDZIEHER 1953). Transient pseudohomosexual relations are observed in man at the beginning of puberty and in old age, in cormorants when less than two years old. Many more similar facts could be added. (See also KORTLANDT 1942, and pp. 191 and 195 in this paper.)

Displacement

A first point in which other principles than hierarchy are involved concerns the so-called "system of drive dispositions" which was postulated in the cormorant and in the avocet (1940 c, pp. 507–514). This system was assumed to be the basis of displacement reactions, i. e. activities in which an impulse sparks over from one instinctive disposition to another one. For example, if in a cormorant or an avocet a fighting impulse is thwarted for one reason or another, the bird will perform sexual and nesting behaviour. Further, if a sexual impulse is thwarted, the bird will peck its mate or make nesting movements. A nesting impulse when thwarted may give rise to sexual or fighting activities. ("Vice-versa principle".) Apparently there exists some nervous mechanism or centre uniting or connecting these three activities and this mechanism or centre was called a drive disposition. In addition to this, there was evidence of an arrangement in levels of such drive dispositions. For example, if in an avocet the fighting impulse becomes stronger while the thwarting also increases, false-incubating may be seen. In situations of highest tension false-sleeping is added to the series. Therefore low-level, middle-level and high-level drive dispositions were distinguished. These systems were shown by means of figures which at first glance might suggest hierarchical systems, but this impression would be wrong.

The factual content of the notion of drive disposition implies nothing more than that an impulse may spark over into more than one motor mechanism. With regard to the causal factors which determine the "choice" of the displacement-reaction we know, at least in some cases, that external stimuli may play a role. (E. g. if there is no nesting material a cormorant will show no displacement-quivering.) In other cases, however, it is essentially impossible to unravel the factors which determine this "choice" because the experimental interference required to analyse them would destroy the specific situation causing displacement. This state of affairs implies that there is *no valid proof at all* of the existence of *internal* factors governing the direction of displacement. It might even be possible, at least in principle, that any impulse may spark over to any motor mechanism and that the "choice" of a particular motor mechanism is determined exclusively by external factors. Considering that, apparently, there are no criteria available either to prove or to disprove the fallacy of this possible assumption, the whole system of drive dispositions as conceived by Kortlandt 1940c must be looked upon as an idle speculation on the internal organisation underlying displacement behaviour.

For the rest, even if the system of drive dispositions held true, it cannot be regarded as a hierarchical system. In common terms the word hierarchy refers to tasks and targets, i. e. goals. The system of drive dispositions, however, is only a discharging mechanism in cases where the proper goals cannot be attained. Performing a displacement-reaction does not solve the problem facing the animal, nor does it terminate the sequence of behaviour that is going on; it only procures a temporary relief. Hence the displacement system cannot be regarded as true hierarchy.

Differentiative development

Another point with regard to which a distinction should be made beween hierarchy and other phenomena refers to the course of ontogenetical development. It is not in all cases that ontogeny proceeds according to the principle of "développement en briques". The additive and integrative type is the rule, it is true, but there are a number of cases in which development proceeds according to the differentiative type described by COGHILL (1929). The most conspicuous example of these is found in the aggressive and defensive behaviour of the young cormorant (KORTLANDT, 1940 b, p. 419):

> "When about 2 weeks old a primitive manner of fighting appears. The young bird begins to stab at strangers, accompanied by loud cries. This pecking or stabbing is obviously feared by fellow cormorants as well as by other species including mammals. At the age of about 4 weeks this stabbing behaviour divides into two actions: (1) The defensive pecking action which is exhibited towards stronger enemies and predators if the bird is caught when fleeing. This action, during further ontogeny, gradually develops into the (so-called) ôôôôô-reaction. (2) The offensive pecking action by means of which territory trespassing cormorants are driven out and even pursued. This performance develops into the common fighting activity. The splitting up of one activity into two different ones with different functions might be called differentiation."

The ôôôôô-reaction mentioned above may be considered in certain respects just the contrary of common fighting: it expresses the utmost fear and distress, whereas true fighting expresses the utmost courage, anthropomorphically speaking. Between these two extremes there is no hierarchical connection of course: their goals are opposites. Now it is an interesting feature that in this case (and, it would seem, in a few other cases as well) the *differentiative type* of ontogeny of behaviour patterns *does not* create a hierarchical organisation of behaviour, whereas the *additive and integrative type* of ontogeny as a rule *does*. This point will require consideration in future research.

Locomotion

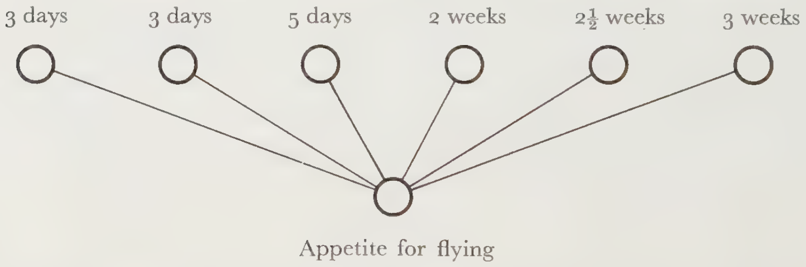
A third point to be examined now concerns the special status of locomotion in the organisation of behaviour. It is a common saying that all instincts make use of locomotion in order to attain their respective goals. In such sweeping terms, this statement is definitely wrong. Many instances are known of, say, ground-living birds which are unable or practically unable to make use of their flying powers in order to escape from danger when driven into a corner. In such situations flight appears to be thwarted. Moreover, during ontogeny a passage of time is required to put the newly acquired flying abilities into the service of the major instincts.

> "When 7 weeks old a young cormorant performs its first flight[1]. In the beginning (after fledging) the young bird uses this motor mechanism exclusively as a goal in itself or as a means to fly from its nest to the water and vice versa. If human beings approach such a newly-fledged young bird, it will look very frightened but it will not fly away. This will not be done until some days later. Still later, the young bird will begin to employ its flying capacities in order to fly to its parents and beg for food. Not until 2 or 3 weeks after fledging will the young bird, when begging, begin to follow its parents in the air. Apparently each new application of flying has to be learned or to mature separately. In cases of extreme urgency, however, the young bird appears to be able to do so much earlier, and if its nest is approached very closely by human beings it will jump out and make flying movements even before being able to fly. But, if a strange cormorant attempts a raid and tries to drive the young out of its nest, the young bird will be pecked to death rather than jump or fly out." (1940 a, pp. 399–400). In this connection some other instances were mentioned in which a bird appeared to be unable to make use of an existing motor mechanism.

By including data which have been worked out since the earlier paper, a scheme can be drawn up demonstrating how the flying abilities in the young cormorant are gradually put at the service of the major appetites, supposing that the strength of the urge is moderate. (Fig. 7.)

Fig. 7. Average date after fledging at which a young cormorant will use its flying abilities in order:

to flee from danger (man at 10 m. distance)	to beg for food (parent is perching)	to have a drink (when thirsty after being fed)	to follow parent in the air and beg for food		social following to fishing grounds
			(flying straight)	(flying in curves)	



It may be added that a similar course of development has been observed in other locomotory mechanisms as well. Further, the same type of development has been found also in man (Gesell 1954).

The general principle appears to be the same as in maturation of a hierarchical system, viz. the subsidiary motor mechanism initially matures as an independent pattern ("en brique") and later on it becomes subordinate to a major appetite. The resulting organisation, however, might be called a topsy-turvy hierarchy: in this case, in consequence of integration, during ontogeny the number of "bosses" of a subsidiary mechanism *in*creases, whereas during ontogeny of a hierarchical system the number of subsidiary mechanisms *in*creases, but the number of "bosses" *de*creases. Further, the branches now point upward, instead of downward as in a hierarchy. For the rest it seems to be a very important fact that notwithstanding these differences, *in both cases* VON MONAKOW's principle holds good.

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[1] Erroneously in the original paper the age was stated 2 months.

It is no wonder that all these findings gave rise to a new prospect of the aims and objects of animal psychology. At that time in continental European psychology (including the McDOUGALL school of animal psychology) the dogma of wholeness often led to a discouragement of analytical research. The ethological school, on the other hand, while opposing this tendency, overshot the mark and hindered the way leading to the research into such phenomena as hierarchy and integration by arguing that: "Instinct is a mere word. Statements can be made only about the instinctive *activity*." (LORENZ 1937 a, p. 289, translated.) In this controversy the programme of animal psychology was explicitly stated by KORTLANDT (1940 a, p. 400) as follows: "Neither the activities nor the behaviour of the animal is the main field of study of the animal psychologist, but simply the co-ordination which is found between these two."

The McDOUGALL *link*

In the course of the following years the idea of hierarchy seems to have become fairly well accepted by the adherents of "hormic psychology" (i. e. the McDOUGALL school) in Holland. PORTIELJE (1942, 1948) has been paying increasing attention to it, at the same time acknowledging the results previously accomplished in this field by human psychiatry and neurology (q.o. RÜMKE 1933). Moreover, in his account the relationship between hierarchical organisation and integrational development in ontogeny was recognised. VAN WIMERSMA GREIDANUS (1946), in his book on instinctive behaviour in man, distinguished a nearly unlimited number of sub-instincts including the distinction between "Kontrektationstrieb" and "Detumescenztrieb" previously made by MOLL in 1898. For the rest, however, PORTIELJE and GREIDANUS remained loyal to the McDOUGALL doctrines by postulating as many primary sub-emotions as there are sub-instincts. To an unbiassed reader it will seem difficult to see the consistency of this, considering that in McDOUGALL's argument the *limited* number of instincts has always been based upon the *limited* number of primary emotions that could be discerned by means of introspection. As a matter of fact the discovery of hierarchy is an achievement of the objectivist analysis of behaviour and it is certainly *discrepant* with the evidence provided by introspection. To quote **Sherrington**: "In this world Mind goes more ghostly than a ghost."

Research on specific hungers

Apart from the authors mentioned above, another trend of research leading to the recognition of hierarchy and to a link between animal and medical psychology has developed in the New World. Unfortunately, owing to lack of personal contacts, it is difficult for European investigators to keep abreast of American scientific trends. Nevertheless an attempt will be made here to draw an adequate picture, although the writer apologises for its shortcomings.

In 1932 **Tolman** wrote "Only the hungry animal seeks and eats food." (loc. cit., p. 274). At the same time, however, **Tolman** recognised that different kinds of food exert different motivating effects. Further, from about 1928 onward, in America as well as in Europe, a gradually increasing number of papers was published dealing with food preferences in animals and man. Their number has grown to such an extent that it is impossible to summarise them here. A valuable review has, however, been given by **Young** (1941).

As a result of these investigations it was recognised that at least in mammals, a fair number of "sub-hungers" related to specific physiological needs can be distinguished (e. g. a hunger for proteins, a hunger for carbohydrates, a hunger for fats, several hungers for minerals and vitamins, etc.). It was also recognised that even a fully satiated animal (or man) can be induced to eat more if an appropriate menu technique is applied. (This fact, in parenthesis, was already known to any good cook but had never been proved scientifically!) **McDougall**'s suggestion, according to which hunger and thirst have to be considered as two sub-drives of one single instinct, appeared to be less absurd than it had seemed previously. As a result of these investigations, in veterinary animal psychology increasing attention was given to the food preferences and feeding behaviour of domestic cattle. In short, with regard to the so-called "physiological" (i. e. homeostatic) needs, the principle of a hierarchical organisation of instincts became fairly generally accepted.

Further, it was recognised that, apart from physiological needs, a number of sub-drives could be distinguished which are directed toward specific consummatory *acts*. In rats it was proved that hunger can occur after stomach extirpation, or if all afferent nerves leading from the stomach to the CNS were severed. Thirst too, appeared to depend upon tissue factors as well as central nervous factors. With regard to food-seeking in chickens **Wolfe** and **Kaplon** (1941, p. 361) concluded: "Amount of reward and amount of consummative activity were separable factors influencing the acquisition and utilization of learning in chickens; effect of amount of consummative activity was greater than that of amount of reward." Moreover, HARLOW (1950), and HARLOW et al. (1951) found evidence of a "manipulatory drive" and other subordinate drives in apes and monkeys. After arguing that there exist more drives than hunger, thirst and sex, he added: "We do not believe that monkeys, apes and men are the only deviant mammals with regard to current motivational theory." (1951, p. 138). Other references from American authors on the hierarchy of food-seeking behaviour have been quoted in this paper on p. 206. With regard to other instincts, however, the idea of a non-hierarchical, or atomistic, arrangement was maintained.

MASLOW'*s conception*

It seems to have been MASLOW (1943 a) who, for the first time in American animal psychology, realised the universal applicability of the principle of hierarchy and who at the same time recognised its bearing on psychoanalytical and general psychology. According to his account: "We should give up the attempt once and for all to make atomistic lists of drives... Such listings are foolish also because drives do not range themselves in an arithmetical sum of isolated, discrete members. They arrange themselves rather in a hierarchy of specificity. What is meant by this is that the number of drives one chooses to list depends entirely on the degree of specificity with which one chooses to analyze them. The true picture is not one of a great many sticks lying side by side, but rather of a nest of boxes in which one box contains three others, and in which each of these three contain ten others, and in which each of these ten contain fifty others, and so on." (loc. cit., p.88). The resemblance to KORTLANDT's picture of "concentric" circles representing appetites, as shown in Fig. 1 in this paper, is striking indeed.

In the quotation just cited, the term "hierarchy" is used in the same sense as has hitherto been done in this paper: a hierarchy of drives ultimately implies a hierarchy of goals apparent in behaviour. Elsewhere in MASLOW's paper, however, the term "hierarchy" was used in quite another connotation: "Wants seem to arrange themselves in some sort of hierarchy of prepotence" (p. 88) which statement means that they will emerge in a fixed order. (For example, in man, at a low level of satisfaction, hunger and similar basic needs will dominate consciousness. If hunger is satisfied, the safety needs will emerge. After having satisfied them, love needs will appear, then the need for esteem and finally the need for self-actualization, according to MASLOW's account.) It will be clear that the term "hierarchy" as used by MASLOW in this second sense refers to the degree of actual urgency, hence not to a postulated underlying system of instincts, or drives. Therefore, in this paper the term "hierarchy" in its second sense may be left out of consideration.

Another terminological difficulty is that in MASLOW's paper the term "appetite" indicates something like a sub-need in the hierarchical system (meant in the first sense). For example there exists one "hunger" for food, but several specific "appetites" for different kinds of food. Further, in MASLOW's account, a "hunger" is based upon a definite physiological need, whereas an "appetite" can be innate as well as acquired. It will be remembered that in KORTLANDT's terminology, on the other hand, the term "appetite" means about the same as instinct and has been used in order to prevent confusion with other connotations of the vague word instinct. These terminological features should be carefully borne in mind when reading MASLOW's papers dealing with these subjects.

Up to the present we have quoted only MASLOW's notion of hierarchy as such. The psychoanalytical concept of hierarchy towards which MASLOW builds a bridge, contains much more, viz. an elaborate conception of ontogeny. This aspect is dealt with in the following passage: (loc. cit., p. 89) "As we go up the phylogenetic scale there is a steady trend toward disappearance of the instincts no matter how we define them[1]. For instance, in the white rat it is fair to say that, by our definition, there are found the hunger instinct, the sex instinct, the maternal instinct. In the monkey the sexual instinct has definitely disappeared, the hunger instinct has clearly been modified in various ways and only the maternal instinct is undoubtedly present. In the human being, by our definition, they have all three disappeared, leaving in their place conglomerations of hereditary reflexes, hereditary drives, autogenous learning and cultural learning in the motivated behavior and in the choice of goal objects. Thus if we examine the sexual life of the human being we find that sheer drive itself is given by heredity but that the choice of object and the choice of behavior must be acquired or learned in the course of the life history." In other words, according to MASLOW, in the human being, drives represent rather unshaped and uncanalised amounts of nervous energy, and during ontogeny the systems of behaviour become built up from their lowest components, by ascending stages, due to object finding, goal finding, and integrational processes. In these ideas we clearly recognise the psychoanalytical conception as set forth in Chapter I of this paper (points 1–4).

Curiously enough, MASLOW pays no attention to the ontogeny of hierarchical behaviour systems in those animal species in which such systems are largely or wholly innate, or grow by endogenous maturation. One might say, therefore, that he has failed to construct the middle span of the bridge uniting animal psychology and psychoanalysis. This point, and other aspects of MASLOW's highly interesting "general-dynamic theory of motivation" which partly lie outside the scope of this Chapter will be dealt with in Chapter IV of this paper.

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[1] In an explanatory note MASLOW makes it clear that he bears in mind only the current American terminology according to which the word instinct refers to innateness, or heredity, and not to drive, or urge.

Relation between maturation, integration and variability reconsidered

In the considerations put forward in this Chapter, one main feature has remained rather obscure, viz. the relationship between the intensity of the "drive" and the integrational level of behaviour resulting from it. This point has been dealt with in a paper (KORTLANDT 1949) which was concerned mainly with the "texture" of behaviour, that is to say such phenomena as co-ordination, integration, regulation, canalisation, interaction, linkage, subordination, inhibition, hierarchy, and so on. The study of these phenomena has led to a more generalised view with regard to the integrational level of behaviour[1].

Before considering the point now to be discussed, it will be necessary to point out that the term "drive" unfortunately has a double meaning. If, for example, an incubating bird shows signs indicating that it wishes to be relieved from duty by its mate, it is said that its incubating "drive" is weak, or low. If the relieving mate, on the other hand, shows signs of eagerness to incubate, it is said that its "drive" is strong, or high. Used in this way the term "drive" means something like actual *impulse*, or *urge*, or *mood*, and the strength of the "drive" may fluctuate from minute to minute or even from second to second. Further, the "drive" (in this connotation) will be exhausted or consumed or satisfied by, for example, the performance of a consummatory act. Another meaning, however, is given to the term drive if a statement is made to the effect that the incubating "drive" is weak or low during the first two days of the incubation period and strong or high during the following days until the eggs hatch. In this case the term drive means something like *tendency* or *inclination*, or the *average* of all actual impulses during the whole day. In this sense the strength of the "drive" may fluctuate from one day to another, or from one week to another, and it will be extinguished after the young hatch, or perhaps a week after hatching. (It will be clear that the term drive in its first meaning [impulse] is about identical to HEINROTH's concept of Stimmung, whereas the term drive in its second meaning [tendency] is *not* identical to HEINROTH's concept of Bereitschaft, although of course the Bereitschaft also depends on the strength of the tendency.)

Now one might argue that the distinction here is trifling. In reality, however, it is the key to a mass of facts. If, for example, in an incubating cormorant the "drive" (tendency) is fairly weak but the "drive"

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[1] The 1949 paper can be considered a second step toward realisation of the task and programme of animal psychology as stated in 1940 a. (This present paper, p. 185). It was based mainly on observations made in 1939, the working out of which had been delayed owing to war circumstances. In the future a much enlarged English edition will appear. The term texture was introduced as a technical term indicating the operative organisation of behaviour.

(impulse) is fairly strong, the eggs will be incubated but nevertheless will remain fairly cool. If, on the other hand, the "drive" (tendency) is rather strong but the "drive" (impulse) is rather weak, the eggs will be kept warm. This difference is due to a difference in degree of maturation. Another example: in immature nesting behaviour, relatively short twigs are used, relatively many quivering movements are made, and these have comparatively little success as far as fastening is concerned. In low-intensity mature nesting, on the other hand, the twigs are longer and there is less quivering, but the fastening-in results are better. Many other similar examples could be given. It is the same principle as has been referred to in the footnote p. 181 in this paper. In other words, the strength of the tendency exerts quite a different effect upon the co-ordination and integration of behaviour as compared to the effect caused by the strength of the actual impulse. Or, it might be summarised as: *The intensity of the tendency is correlated to* (and presumably determines) *the level and purposiveness of behaviour, its degree of integration and canalisation, the selectivity in choosing its objects, and the setting in motion of the pair-forming processes* such as initiating the reproductive cycle, settling down in a territory, or falling in love with a mate. Or, formulated more briefly, quantity and quality of behaviour go hand in hand (KORTLANDT 1949, pp. 15, 26, 27, 31, 73, 78, 82, 85, 87, 90, 95, 100, 107, and Appendix). In this last sentence the word "quantity" refers exclusively to the tendency, or daily average of impulses, and not to the actual impulse itself. The intensity of the impulse may sometimes even have a contrary effect, as is shown by disintegrative phenomena which are due to an excess of drive, for example in vacuum and displacement activities.

The apparent relation between the strength of the tendency and the integrational level of the resulting behaviour is a matter of observation. An explanation may be offered by attributing this phenomenon to hierarchy. If the tendency originates from a relatively high level in the hierarchical system, a relatively large number of appetites will contribute to it. Consequently, the resulting tendency will be proportionately strong. At the same time the large number of participating appetites involves the possibility of utilising a correspondingly large number of subordinate motor mechanisms, which fact creates a base to attain a relatively high degree of integration. A glance at the schematic drawings in this Chapter will suffice to clarify the principle. Further, the *combination* of the innate releasing mechanisms of the behaviour patterns involved will naturally be more selective than any isolated releasing mechanism.

This tentative explanation finds support when considering the variability of behaviour. During ontogeny and seasonal maturation the level at which variations are found will increase to the same degree as the motivational level increases. In the very first stage of development there is still no rigidity in the so-called fixed patterns, or Erbkoordinationen. (All contrary statements on rigidity as made by ethologists do not account for ontogeny.) For example, in a cormorant when two or three weeks old, quivering is an irregular movement and kee-kee-gargling is performed in an irregular rhythm (1940 b, p. 429). At this stage the behaviour looks clumsy, just as in a young puppy. At a later stage the fixed patterns have become almost perfectly rigid but there is much variation in the way in which the bird makes use of them, or combines a number of them into one activity or series of activities, and thus, in human eyes, the behaviour acquires a playful character. When full maturity is reached in the behaviour system under consideration, little variability is left in the lower and middle levels, but there may be great variability in the choice of the means by which the top-level goal can be reached, at least so far as these variations will suit the purpose. (See Fig. 5!) It appears, therefore, that the "*zone of variability*" in behaviour *ascends in the same degree* as does the progress in maturation. Descriptions of ontogeny given by BINGHAM (1928), EIBL-EIBESFELDT (1950, 1951), and SAUER (1954) suggest that the same principle applies also to behavioural development in the chimpanzee, the badger (*Meles meles* L.) and the squirrel (*Sciurus vulgaris* L.), and to the development of song in the whitethroat (*Sylvia c. communis* LATHAM). When in the course of development the top-level has finally been reached, variability may look like an over-riding intelligence, although actually we are dealing with a simple hierarchy of instincts. At this final stage the cormorant's behaviour has become "serious" in human eyes. Apparently the gradual shift from "clumsiness" via "playfulness" to "seriousness" and "intelligence" is not so much a shift in the essential *nature* of behaviour as a shift in the hierarchical *level* from which the tendency originates. Perhaps it is only our own human nature that imagines a change in the essential nature and character of behaviour. To a child, "play" is extremely serious. In every-day life "mental maturity" is usually regarded as a matter of experience and wisdom but there might be more reason for considering it a matter of hierarchy of instincts, in animals as well as in man. It may be added that human imbeciles are known to be very cunning if a strong tendency (e. g. nostalgia or sexual desire) is activating them.

In other words, at least in the cormorant, normal variability of behaviour proceeds mainly at a level *just below* the highest appetite which is activated at that moment. Maturation of a higher appetite largely suppresses variability at the lower levels. This process cannot be ascribed to conditioning or learning, for during seasonal "dismaturation" or in cases of ill-health or trauma the reversed sequence is observed and variability descends to the lower levels. It therefore seems that normal variability of behaviour is a biological function exerted mainly by the highest activated tendency, *in order to accomplish integration and adaption* of behaviour as circumstances require. (See also Chapter IV, § 3, p. 253.) A tentative suggestion of about the same tenor has been made already by Freud (Ges. Werke V, p. 139; Stand. Ed. VII, p. 237). According to his surmise, some cases of perversion in man that are due to a lack of integration, may find their root in a hereditary weakness of the top-level instinct which thereby is unable to accomplish the integration of the lower instincts. In the cormorant, the tentative presumption according to which the level of the tendency has to be considered the primary cause, and the degree of integration its consequence, finds support in a few observed cases in which "quality" apparently lagged behind "quantity" of behaviour. (See also Chap. IV, § 4, p. 256.) It is interesting to see that the study of integration in both animal species results in essentially identical conclusions.

Inference of hierarchy from characterological evidence in the cormorant

This last point leads us to the so-called "characterological approach" or "symptomatic analysis", which is a third way of arriving at the idea of hierarchy and which was applied in the 1949 paper in addition to the two ways of approach described in 1940-a and mentioned earlier in this paper. A few words may be said now on this third way of approach to hierarchy. The following example will illustrate the principle.

In the pair-forming period a normal mature female cormorant usually produces panting sounds which are quite different from the croaking sounds produced by the male throughout the year and by the female out of the pair-forming season. Further, a normal female during the pair-forming period will as a rule behave in a submissive way toward males, will not bring nesting material to the nest, shows no wing-flapping (i. e. masculine advertising display) or displacement-wing-flapping, and will not act as the mounting bird in copulation. There are, however, a substantial number of females who do perform such masculine activities. Among them, the majority is composed of females who show *most* or *all* of these masculine activities without any apparent external cause. Evidently these females are characterised by a bisexual disposition in their temperamental make-up and this determines the occurrence of the *whole set* of masculine activities. In other words, the co-incidence of a *group* of symptoms points to a *hierarchical* texture to which all these activities are subordinate. The same co-incidence of symptoms is observed when, after the pair-forming season, normal females regain the masculine traits which are shown by them during the rest of the year. In medical language one might speak of a syndrome. In the paper referred to, the term *garniture* or *set* of activities was introduced.

By the same argument it would seem that among males too, a number of individuals have to be regarded as bisexual. Zoo-observations amplified by field-data have shown that, apart from seasonal variations and some external factors which may shift behaviour into a more masculine or more femine direction, as a rule the bird's temperament will remain constant year after year once a certain age has been reached.

An important fact is that bi-sexual females prefer to mate with bi-sexual males, and vice versa, whereas extremely feminine females prefer to mate with extremely masculine males, and vice versa. Apparently in its behaviour the bird gives expression to its psychological attitude towards possible marital partners. In other words, the more masculine or more feminine way of behaving is an expression of the "characterological" aspect (or perhaps "personality") in the goal the bird is striving for, viz. its preference to mate with a certain type of marital partner. Moreover, careful observation shows that potential marital partners clearly understand this meaning of pair-forming display. If, however, a male or a female is unable to find a suitable partner (e. g. owing to the law of supply and demand in the marital market), in the long run it will adjust itself according to circumstances, at least within certain limits[1]. To explain these phenomena, the principle of threshold-lowering is not sufficient. A consistent and sound explanation is arrived at by postulating a top-level appetite (viz. the appetite for being paired, or something of a similar nature) which is supposed to govern *both* sets of activities. In other words the masculine and feminine tendencies in the cormorant are considered to represent two sub-appetites which are hierarchically subordinate to a top-appetite directed toward the formation of a marital bond. Thus there is no need for a casual explanation with regard to marital adjustment and pseudo-homosexuality. Here again the essence of hierarchy appears to be a hierarchy of *goals*. For further remarks on this point the reader is referred to KORTLANDT (1953).

The distinction between masculinity and femininity is only one aspect of cormorant characterology. The other main aspect is the distinction between individuals which are characterised by a more active or by a less active temperament. This second distinction is at the same time a distinction between individuals which are characterised by a relatively high degree of integration in their behaviour and those which are characterised by a relatively low degree of integration. An example may suffice to illustrate the principle: The only case ever observed of a male cormorant who performed wing-flapping (i. e. advertising for females) while in the sleeping posture, was observed in a male with the most lethargic temperament ever studied. (Possibly the bird was dreaming.)

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[1] In captivity, if there is a lack of members of the opposite sex, an almost complete inversion of sexual and pair-forming behaviour may occur. With regard to similar cases MORRIS (1952) has used the term homosexuality. This usage of the word is wrong according to customary medical terminology, at least on the European continent. In cases of *adaptive* inversion the terms pseudo-homosexuality or sexual ambipotency should be used. In cases of *spontaneous* and *immediate* inversion towards certain members of the same sex or in special circumstances, the term sexual ambipotency seems the only appropriate one. The term homosexuality should be used only in cases of *innate* and *complete* inversion.

For the rest, the phenomena dealt with here should not be confused with displacement-activities or with activities in which a masculine pattern *during evolution* has been transferred to and ritualised in the normal feminine behaviour system, or vice versa. This last mentioned category has been called "*derivative activities*" in KORTLANDT's terminology (1949) and they constitute a sub-group of the "*derived activities*" discerned afterwards by TINBERGEN (1952) who, when coining this term, did not refer to the pre-existing term resembling it. In these matters confusion may easily arise and therefore a very exact employment of terms should be recommended.

In cases like this it again appears that there exists a marked correlation between the strength of the tendencies on the one hand and the degree of integration on the other hand, except in a very few individual cases in which the "quality" of behaviour lagged behind its "quantity". Further, the selectivity toward objects and the aptitude for pair-forming processes, again appear to be dependent upon the strength of the tendencies. In other words, the study of cormorant characterology leads to conclusions exactly convergent with those that have been obtained by studying ontogeny, maturation and "dismaturation".

It would take too long in this paper to set forth more fully the outstanding importance of temperamental factors with regard to the individual's fate and destiny. It may be remarked only that, when applying symptomatic analysis, an extensive amount of observational data covering the whole reproductive period is required together with careful and painstaking analysis of these data. Notwithstanding these handicaps the characterological approach has appeared to be the most rewarding of the three approaches to hierarchy and other concepts concerning the texture of behaviour.

Up to here, our attention has been chiefly focussed on the innate characterological factors involved in the integration of behaviour. It must be added, however, that during ascending development, acquired components play a role as well. These also are revealed by applying the characterological approach. The following quotation may illustrate this point:

"It had struck me that in all parts of the colony with high nests only a few ringed birds were to be seen and that in sections with low nests many ringed ones were found. This was the more surprising because in the course of years the birds inhabiting low nests frequently moved to and fro from one side (of the lake around which the colony lies) to the other. Apparently the same group of ringed specimens kept on moving. Needless to say, nearly all nestlings which could be provided with rings, originated from the low trees in the colony. Therefore I concluded that the birds hatched in high nests will breed in high places and those hatched in low nests, in low places; even if, during moving, they overcome their attachment to the native place... Apparently the birds always looked for a landscape resembling their hatching site, just as, according to Freud, man in cases of love, friendship and enmity is often dependent on resemblances to persons who played a role in his earliest years... Cormorants of low origin will usually breed low and continue to breed low, even after moving. This implies that a cormorant is attached not (or not exclusively) to its native spot as such but also (or exclusively) to the type of landscape in which it grew up." (KORTLANDT 1942, translated from pp. 253 and 270; see also 1949, p. 81.) This statement was proved at least for the males; with regard to the females, however, the statistical figures were less conclusive.

From these and similar facts it appears that, during individual development, the *innately proceeding* process of ascending integration is *attended by* an intermingling or even an amalgamation of innate and acquired components, especially on the sensory side of behaviour. Other suggestions on this point have been given by THORPE (1951, p. 264), who approaches the same problem from the point of view of imprinting phenomena. In Chapter IV, § 2, we shall consider what may happen if in the integrational process innate and acquired components appear not to fit in with each other.

Validity of the new conception

Compared to the papers published in 1940, the new formulation summarised above provides a more general conceptual frame for the phenomena referring to hierarchy, maturation, dismaturation and so on. The new concept has appeared to be valid in a great number of instances from observational data, partly published in 1949, but for the most part still unpublished. The concept has appeared to be valid not only in the cormorant but in other animals as well. For example, in the Great Crested Grebe (*Podiceps cristatus* L.) Miss H. A. W. SMIT found that immature birds perform all the usual courtship activities, but often in a wrong sequence, or in ceremonies in which these activities do not belong, or toward the wrong sex (unpublished M.S.). Similarly sticklebacks (*Gasterosteus aculeatus* L.) in the maturation and dismaturation period preceding and following a reproductive cycle show many irregularities of behaviour, such as sand-digging at scattered points, disintegrated building activities, and so on. (Verbal communications of VAN IERSEL and SEVENSTER, and observations of the present writer.) Accurate descriptions of the ontogeny of behaviour in mammals and birds leave no doubt that ascending development is the rule, differentiative development the exception. (See e. g. EIBL-EIBESFELDT, SAUER, and many studies on rats and chimpanzees.)

In the new concept PORTIELJE's findings on "differentiation" and "symbolisation" can be arranged more appropriately than in the old one, and the same applies to the integration of flying abilities as shown in Fig. 7 and similar phenomena. There is evidence that the concept holds good not only for birds and mammals (including man) but also for lower vertebrates, as indicated above. There are reasons for assuming that a still further generalisation of the principle will be justified, and perhaps there are possibilities of practical application in hormone therapy. (See GOLDZIEHER and GOLDZIEHER 1953.) This last point is also suggested upon grounds derived from cormorant characterology.

An interesting point which may have important theoretical implications is the *discontinuous* course of integration which has been found in several behaviour patterns during ontogeny and maturation, and which is suggested also by some characterological facts. In some maturation processes a continuous increase of the tendency will lead to a step-by-step increase of the integration, like climbing a staircase. In some other processes an increase of the tendency will at certain levels cause a temporary drop in integration, followed by a re-integration at a new and higher level. In all such cases one may speak of "developmental jumps" (KORTLANDT, 1949, pp. 15, 26–27, 85–87; see also Chap. IV, § 2, pp. 237–240, in this paper). The total number of successive developmental leaps in one behaviour system in the cormorant may amount to five, which number has been found characteristic for the ontogeny of the tendency toward individuation during the first three months of life. The occurrence of such jumps seems to provide fairly firm ground for the assumption of *distinct* hierarchical levels, as have been assumed in the drawings in this Chapter. Where, however, no development of integration by jumps is observed, the idea of distinct levels may be only an illusion and the schematic diagrams therefore too rigid. In the latter category one might even doubt whether the term hierarchy is fully justified. At present a definite statement on this point seems unwarranted. (See also pp. 160–161.)

In this connection it should be borne in mind that the relation between the strength of the tendency on the one hand and the degree of integration on the other hand is still a somewhat enigmatical matter. It is true, a high level tendency disposes of more motor mechanisms than a low level one disposes of, and this datum explains why a higher degree of integration *can* be attained, but it does not explain why a higher degree of integration *is* attained in perhaps 95 or 98 per cent of all observed cases in which an inference could be made, for we must distinguish between the possibility of integration and the realisation of integration. Moreover, it remains enigmatic how the variability of behaviour is advanced at a level just below the highest activated tendency, but at the same time suppressed at the lower levels. These questions are of the utmost importance because of their bearing on human psychotherapy and psychiatry but at present it seems impossible to give even an approximate answer to them or to suggest a way of future research. In Chapter IV we will return to some aspects of these questions.

III. THE IDEA OF HIERARCHY IN ETHOLOGICAL ANIMAL PSYCHOLOGY

In the foregoing Chapters two important trends of thought with regard to the idea of hierarchy have been recognised: a positive one, originating from medical sciences and starting with JACKSON and FREUD, and an initially tentative one, originating from hormic psychology and starting with LLOYD MORGAN and McDOUGALL. In animal psychology, from PORTIELJE and MASLOW onwards, both trends have since been united. In the ethological branch of animal psychology, however, scientific thinking concerning hierarchy started with a rejection of the idea.

Hierarchy rejected by Lorenz *and* Tinbergen

In 1935 Lorenz wrote: (translated) "In animals, or at least in birds, I cannot see any possibility of distinguishing between high order instincts and low order instincts as has been done by McDougall. The great independence which is a characteristic of the separate participating actions in a functional cycle implies that the apparently less important of them are in reality as important mosaic elements with regard to the functioning of the whole as any of the others. If we want to make a statement on the accompanying emotions and feelings then we have necessarily to postulate as many mutually independent kinds of emotions as we can find autonomous instinctive actions" (i. e. Erbkoordinationen) (loc. cit., p. 385). It will be clear that in this statement even the simplest type of hierarchy is rejected. Each Erbkoordination is supposed to work for its own sake, or atomistically. In parentheses, Lorenz's quotation of McDougall is not quite correct, as has been shown in Chap. II.

Another interesting point is that in order to denote the postulated *action-specific* emotions or feelings Lorenz (pp. 384–385), referring to Heinroth, proposed to use the term mood (Stimmung). It is curious to find that this technical term was originally intended to have a definite subjectivist connotation and that thereby the McDougall link was explicitly maintained in the concept of instinct as defined by Lorenz in 1935 (loc. cit., p. 384), although at the same time the existence of instincts higher than bottom level (either driving agents or generators of emotion) was rejected. The *only difference* between the concepts of "mood" and "emotion" was a difference in hierarchical level.

In subsequent papers by Lorenz (1937 a, 1937 b), and Lorenz and Tinbergen (1938) mood was redefined as an objectivist concept indicating the internal, i. e. physiological, readiness of the animal to perform a specific instinctive action in a given stimulus situation. Fluctuations in this reactive readiness, viz. reaction-specific exhaustion, threshold-lowering and vacuum-activities, were ascribed to hypothetical reaction-specific stimulus generating substances of neurophysiological origin (reaktionsspezifische Erregungsstoffe). Further, the instinctive motor patterns or fixed action patterns (Erbkoordinationen) showing these fluctuations in reactive readiness were made equal to the nervous automatisms which at that time had just been discovered by von Holst (1935 and later years). One might even suggest that the direction in which Lorenz's ideas on instinct evolved was largely influenced by the progress of neurophysiology[1]. From the sociology of

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[1] For example, the term Leerlaufreaktion (indicating both spontaneity and reactivity of behaviour) is a typical contradiction in terms and can be understood only if

(see cont. p. 198)

science it is known that such relations between different sciences often occur and that as a rule scientists are not conscious of them. TINBERGEN's statement (1951, p. 72) that "the work in the two fields was done independently" does not take into account such hidden influences from one science to another. In fact it seems that neurophysiological orientation in ethology has hampered the recognition of hierarchy, in exactly the same way as the former reflex theory hampered the recognition of spontaneity in behaviour.

Owing to these tendencies in ethological thinking, the idea of hierarchy was pushed more and more out of sight. No other hierarchical level of instincts except bottom level was recognised. The animal was considered to be an atomistic conglomerate of fixed patterns, each equipped with its own reaction-specific energy and its own appetitive behaviour but without any co-ordinating mechanisms governing them, except mutual inhibition at bottom level.

Hierarchy rediscovered by BAERENDS *(1941)*

In 1941, however, hierarchy was rediscovered when BAERENDS found evidence of a rather complicated system of moods in the female digger wasp. Four levels of moods were distinguished, with the restriction that with regard to the highest level (the parental mood) only indirect arguments were available. Each mood was characterised by the fact that a female digger wasp when in this mood tends to perform any one activity of a *group* of activities, or may be easily induced to perform any of these activities. Subordinate to each mood (except the bottom level) a number of lower order moods was distinguished, representing in their turn a more specific readiness for a sub-group of activities, or for a single activity.

An essential feature in BAERENDS' account is that mood was defined as "a condition (of the animal) in which internal factors determine the direction of behaviour" and that "it is not at all easy to get a wasp out of her mood" (translated, loc. cit., pp. 199 and 201). A hierarchy of moods therefore means a hierarchy of *internal driving* factors. Further, BAERENDS links up the concept of mood with the concept of appetitive behaviour when stating: "It seems indeed that each mood has its own appetitive behaviour, and this applies to the first order mood as well as to

(cont. note p. 197)
one knows that it was formed in an earlier period when LORENZ was an adherent of ZIEGLER's reflex theory. Further it is an interesting fact that LORENZ's successive papers in those years paid increasing attention to vacuum-activities and allied phenomena in the same degree as the progression of VON HOLST's investigations. In ethological interest there has been a gradual shift from "stimulus" to "drive" and from external to internal causes. This shift seems to have followed up a preceding similar shift in neurophysiology.

the second, third and fourth order moods." (Translated, loc. cit., p.206.) Consequently a hierarchy of moods is at the same time a hierarchy of appetitive behaviour patterns. It seems therefore that BAERENDS' concept was almost identical to KORTLANDT's hierarchy of "appetites", although the two were conceived independently of each other. Further, BAERENDS did refer to PORTIELJE's work and tried to clarify the points of view taken on both sides.

Actually, however, there is some difference between the formulations as drafted at that time by BAERENDS and by KORTLANDT. In BAERENDS' conception the goal of first-order appetitive behaviour is to put the animal into a situation where it may "choose" between different sets of appetitive behaviour belonging to the second level, and the goal of second-level appetitive behaviour is to make a choice at the third level, and so on. This means that first-order appetitive behaviour is thought to cease as soon as second-order appetitive behaviour starts, and this in its turn is thought to cease at the start of the third-order one. In KORTLANDT's scheme, on the other hand, second-level appetitive behaviour is conceived to form a constituent part of first-level appetitive behaviour because it is employed by the animal as a means to attain the first-order goal. Further, third-level behaviour is considered to be a part of second-level as well as a part of first-level behaviour. (E. g., bringing twigs, inserting twigs, quivering, raiding a nest, etc., are all used as means to satisfy the need for a nest.) Perhaps the difference between the two authors may be only a terminological one but it may also conceal some unseen implications leading to different opinions with regard to the goals for which the animal is supposed to be striving. In this regard a later study by BAERENDS and BAERENDS-VAN ROON (1950) presents no new points of view. For the rest, LORENZ (1954, p. 140) when summarising BAERENDS' conception, used the expression "Ineinanderschachtelung" which term may be considered practically synonymous and homonymous with KORTLANDT's and MASLOW's formulations, whereas BAERENDS' formulation might more properly be called an "Untereinanderschachtelung".

"Hierarchy of causal factors" as conceived by TINBERGEN *(1942)*

The next step with regard to the concept of hierarchy in ethological theory was taken when TINBERGEN (1942) described what he called a "hierarchy of causal factors" in the Three-spined Stickleback (*Gasterosteus aculeatus* L.). In his account, however, an essential feature of the concept as it was formulated by BAERENDS was omitted. There may even be some doubt whether the term hierarchy is fully justified in this case.

In spring a male stickleback will settle down in a suitable territory. Quoting from TINBERGEN's description (loc. cit., pp. 55–56) "the perception of a suitable territory - provided certain other factors are also active - brings the male into a reproductive mood. That is to say, it is ready to fight other males with which it lived in peace during the winter, and it is ready to build a nest, and afterwards, to show sexual behaviour toward females... Given the factors that bring the fish into the reproductive mood, other additional factors decide whether it will come into a fighting or a building "sub-mood". This phenomenon could be described as a hierarchy of moods or of drives... A stickleback in fighting mood is ready to perform several activities, dependent on the nature of external situation. A strange male in the territory evokes an attack; if it flees, the owner of the territory gives chase. If it does not flee, it is bitten. If it fights back, it is attacked with the help of the ventral spines. At the territory's boundary, the presence of a male evokes threatening."

The fallacy of Tinbergen's *conception*

By putting it in this way Tinbergen waters down the concept of hierarchy into a *classification of IRM's* instead of a true *hierarchy of internal driving factors* as conceived by Baerends. In fact nothing else is proved except that chasing is released by the sign stimulus "fleeing strange male inside territory", that biting is released by the sign stimulus "non-fleeing strange male inside territory", that fighting with the spines is released by the sign stimulus "fighting strange male inside territory" and that threatening is released by the sign stimulus "strange male at the territory boundary". Evidently there are common elements in these four *sign stimuli* but no proof is given of a common component in the *nervous mechanisms* responding to these sign stimuli. One might imagine the possibility that their working corresponds to the following scheme: (Fig. 8)

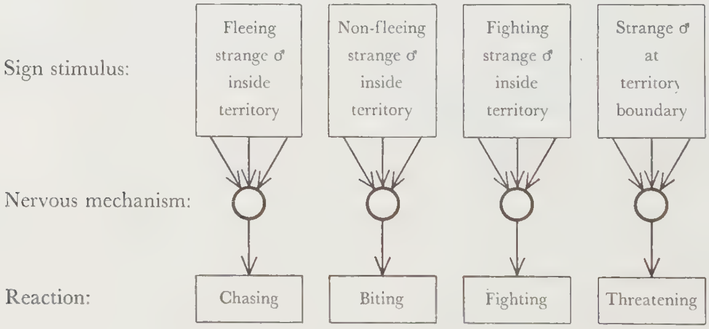
Sign stimulus:
Fleeing strange ♂ inside territory
Non-fleeing strange ♂ inside territory
Fighting strange ♂ inside territory
Strange ♂ at territory boundary
Nervous mechanism:
Reaction:
Chasing
Biting
Fighting
Threatening

Fig. 8

There do exist at least some cases in which we are pretty sure that a common component in the stimuli by which two different forms of behaviour are elicited *does not prove* a hierarchical relation between these two. For example, in male predatory mammals, blood-stains may elicit food-seeking as well as sexual behaviour. Nevertheless it seems quite certain that in this case there is no reason to postulate a superordinate IRM or other instinctive mechanism embracing both food-seeking and sexual behaviour.

Moreover in Tinbergen's account of aggressive behaviour in the stickleback no reference is made to possible internal factors determining the direction of behaviour and no factual evidence is given in favour of a common source of energy or other motivating connections uniting these reactions in the nervous organisation of the animal. Whereas according to BAERENDS a sub-mood may determine the "choice" of the reaction, TINBERGEN (1942) seems to consider this "choice" as being determined exclusively by external stimuli. In his account no indication is given whereby there exists any special interdependency between the four IRM's of aggressive behaviour. It is difficult indeed to see any real difference between this concept and LORENZ's atomistic system of independent instinctive actions lacking superordinate co-ordinating mechanisms higher than bottom level. For the rest, postulating a hierarchy of IRM's based upon common components in their releasing sign stimuli fails to take into account the configurational (Gestalt) character often found in sign stimuli, as far as the law of heterogenous summation (SEITZ 1940) does not apply.

It is true, in TINBERGEN's paper some contradictions may be found pointing to another interpretation taking into account internal factors as well. On p. 58 a statement is made with regard to the fighting drive in the stickleback, according to which "the internal factors decrease the threshold for external stimulation of *all* kinds of fighting activities". At this crucial point, however, no further supporting argument is given. On p. 56 on the other hand, threshold lowering for *all* fighting behaviour is attributed to an *external* factor ("when stimulated by another male"). It seems therefore that in TINBERGEN's view internal driving factors provide at most only an *additional* instead of an *essential* proof of the existence of hierarchy. The criticism made in this paper, however, implies that, on the contrary, the essential feature of hierarchy is a hierarchy of *internal* driving factors urging towards satisfaction, i. e. a hierarchical system of instincts in which each instinct at any level has its own rate of threshold lowering, its own appetitive behaviour and its own goal[1].

For the rest, there are cases in which the type of "causal hierarchy" postulated by TINBERGEN cannot be applied at all. For example, in mature male herons and cormorants all sexual behaviour is restricted to the nesting territory, with the sole exception of copulation itself. Evidently the sign stimulus evoking copulation is in this case more simple than the sign stimuli evoking sexual behaviour in general, instead of being more specialised as TINBERGEN's theory would require; nevertheless there can be no doubt that copulation is a constituent part in the hierarchical organisation of sexual behaviour. (For the sake of completeness it may be added that in the male cormorant, copulations outside the nesting territory are not necessarily due to threshold-lowering.)

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[1] Evidence pointing to a type of hierarchy in which each instinct at any level shows its own *independent* rate of threshold heightening and lowering has been given recently by VAN IERSEL (1953) in his very detailed analysis of the parental drive in the stickleback. For somebody who is not familiar with this species it is, however, not easy to follow VAN IERSEL's argument. The question might be raised whether, in investigations of this kind, argument can be considered complete if not supported and checked by factor analysis, multiple correlation computation, confluence analysis, or other statistical techniques. Apart from these remarks, the impression seems justified that by VAN IERSEL's work (especially on p. 137 and p. 147) good reasons have indeed been produced to assume a hierarchy of instincts in the stickleback, although VAN IERSEL himself judges the existence of a "reproductive instinct" in the stickleback to be still insufficiently proved. (Personal communication.) Anyhow, if we define hierarchy as has been done by BAERENDS, it must be admitted that TINBERGEN has never proved the existence of this type of hierarchy in the stickleback.

Another contradiction in TINBERGEN's paper is that he acknowledges the major instincts as recognised by McDOUGALL and the hierarchy in appetitive behaviour as recognised by BAERENDS to be contributions fitting his own conception of hierarchy. By doing so he overlooks the fact that, in McDOUGALL's concept, a number of instincts are not satisfied by a consummatory act but by a consummatory object or situation. He also overlooks that, in BAERENDS' concept, a hierarchy is defined as a hierarchy of internal factors. It seems therefore that TINBERGEN, by including in his concept of hierarchy all cases of common causal factors evoking different forms of behaviour, intended to generalise the concept more widely than hitherto, for we cannot assume that he was unaware of the essential divergences[1]. It is the present writer's opinion, however, that the concept of hierarchy of instincts ought to be restricted to cases in which there is plausible evidence of a hierarchical organisation of *co-ordinating and integrating factors* active in the nervous mechanisms underlying behaviour. If this restriction is exceeded the concept may lose much of its fruitfulness to analytical research.

Hierarchy of nervous mechanisms not proved by TINBERGEN

In his later papers on the subject, TINBERGEN (1950, 1951, 1952) maintains the essence of his concept according to which hierarchy is proved if two or more reactions are dependent on a common causal factor, either external, internal, or both. At the same time, however, a new element is added to the concept: the common causal factor is now definitely attributed to a *nervous centre* and the presence of such a centre is considered to be proved (or at least rendered probable) on the evidence provided by the behaviour of the stickleback described above (TINBERGEN 1950, pp. 306–307; 1951, p. 103). Further, the concept of instinct is tentatively defined as "a hierarchically organized nervous mechanism" etc. (1951, p. 112). The impression seems justified that this revision of the concept is due to, or influenced by, neurophysiological investigations of WEISS (1941), HESS et al. (1943, 1944), and BRÜGGER (1943) pointing to a hierarchy of nervous centres. Here again ethology seems to follow the lead of neurophysiology instead of taking its own course.

In this connection it may be interesting to consider in more detail the tenor of the neurophysiological evidence[2]. It appears that the investigations just quoted suggest an efferent hierarchy of motor mechanisms, or a hierarchy of factors responsible for threshold lowering, vacuum activities and appetitive behaviour, i. e. a hierarchy of appetites and goals as described by BAERENDS and KORTLANDT. No arguments can be derived from them pointing to a hierarchy on the afferent side of behaviour, or a hierarchy of releasing factors as postulated by TINBERGEN in his more extended concept of hierarchy. Further, HESS himself has always been too careful to make any definite implications or conclusions at these points.

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[1] In order to be consistent, in TINBERGEN's concept, it would be necessary even to include under the heading of hierarchy all cases in which one and the same stimulus causes different reactions (e. g. ambivalent behaviour).

[2] The original papers are so full of data relevant to the problem of hierarchy that no attempt to summarise them will be made here. (See also pp. 210, 212, 247, 257).

In our argument we have now advanced so far as to realise that a common factor found in two (or more) sign stimuli is in itself not sufficient proof of a nervous hierarchy. The same, however, also applies to a common component in *internal* drives. At first glance this point may not be obvious and therefore some explanation should clarify it.

According to TINBERGEN (1952) a "broody" herring gull will perform different actions which "are all dependent on broodiness in general. Broodiness is the state into which the bird is brought by prolactin, and, probably, by some external stimulus as well, but the pattern to which it gives rise is varied and consists of at least three types of response each governed by its own releasing stimulus situation." (Loc. cit. p. 4.)This state of affairs was put forward as an argument pointing to a hierarchical structure in the brooding instinct. One could imagine the possibility, however, that prolactin exerts a stimulating influence upon behaviour patterns which for the rest are working entirely independently of each other, and therefore in this case nervous hierarchy has no more been proved than in the case of the stickleback. Effects like these may be exerted even if there is no CNS at all.

Now of course it is possible to widen the concept of nervous mechanism so far that, for example, prolactin is considered to be a component of a nervous mechanism rather than of a motivational mechanism. Such a possible redefining, however, will have far reaching conceptual implications. A hormone is not an instinct, after all. This point may be illustrated by the following example. It is a well known fact that a man who has drunk too much alcohol will show an increased readiness to laugh, to weep, to become angry, or sentimental, or sexually motivated, and so on. According to TINBERGEN's definition such a state of readiness caused by one causal factor has to be called a mood, and in this case one might speak of an alcoholic mood. Nevertheless, it seems difficult to see in these facts sufficient reasons for postulating a general superordinate instinct provided with an accessory hierarchical nervous organisation and especially susceptible to stimulation by alcohol. Thus apparently a hierarchy of internal causal factors is in itself not sufficient proof of a hierarchy in nervous mechanisms, unless the concept of nervous mechanism were redefined so widely and so vaguely that it would become nearly meaningless. In other words, in TINBERGEN's concept the essential and the accidental features of the notion of hierarchy are interchanged.

Independent of the present writer, HINDE (1953, pp. 198 and 214) has tentatively expressed some of the criticism given above. After having summarised TINBERGEN's arguments pointing to a hierarchy of causal factors, he states: (p. 214) "This hierarchy of causal factors, which can be objectively determined, is exhibited in the behaviour of the animal as a hierarchy of moods... In correlation with the different sets of stimuli to which the animal is susceptible, it shows different types of appetitive behaviour... It seems legitimate to assume that each form of appetitive behaviour is dependent on a particular set of nervous mechanisms, or pattern of nervous activity." Thus, starting with TINBERGEN's conception (viz. a hierarchy of sets of causal factors), HINDE returns to BAERENDS' conception (viz. a hierarchy of sets of appetitive behaviour), at the same time postulating (but not proving) that the last one is correlated to the first one. In this way, however, the actual problem and its logical sequence is turned topsyturvy: definite proof of the existence of a nervous hierarchy can only be given (except by neurophysiological evidence) by proving the existence of a hierarchical organisation in *appetitive* behaviour or by proving the existence of a hierarchy of moods responsible for *appetitive* behaviour. The question whether there is, or is not, a correlation between the "hierarchy of causal factors" on the one hand and the hierarchy of appetites on the other hand has to be considered next. As already mentioned above, when discussing copulatory behaviour in the heron and the cormorant, there are cases in which such a correlation does not exist and then an indirect argument as given by HINDE cannot be maintained.

Ultimately therefore it may be concluded that the concept of hierarchy is appropriate only if, by careful analytical research, evidence is found pointing to a hierarchical organisation in the co-ordinating and integrating factors which are responsible for *directiveness* in behaviour. Such a hierarchy is a hierarchy of factors determining the excitation, course *and* outcome of appetitive behaviour. In other words, hierarchy is essentially not a matter of *drives* but of *goals*. True hierarchy is, so to speak, not found on the primal but on the terminal side of behaviour, as far as such a distinction can be made. By formulating the concept in this way a link is made with its connotation in ordinary language, which implies that in a hierarchical organisation (e. g. a ministry or an army) each branch of service has its own task and target but at the same time receives its directives from the higher levels of the organisation which are in turn responsible for the higher targets consigned to them.

Essence of divergence on hierarchy between TINBERGEN *and* KORTLANDT

It is particularly the *directive aspect* of hierarchy which many ethologists have shown a reluctance to recognise. From CANNON onwards (1st ed. 1915) a vast amount of research has been done on the nature of hunger in general, on specific hungers in particular, and on the motivational effects of general or specific hungers. Nevertheless in 1937-a LORENZ still wrote: "The desire to hunt, the appetite for the instinctive actions involved, occurs absolutely independently of the state of the animal's hunger... A grebe, for example, hunts for hunting's sake and does not perform these reactions more intensively when it is hungry." (Translated, loc. cit., pp. 316–317.) In support of this argument he added that a grebe will die of hunger if it cannot obtain its food in the natural way. (Actually, however, any adult grebe captured in the wild can learn to take dead fish from a food-dish within one or two days, according to this writer's experience.) In 1939 LORENZ even went so far as to claim that not only in animals but also in man the motive for earning one's bread is found in crumbling and biting instead of feeding (loc. cit., p. 87). In 1953 he stated jokingly that a fat man does not go to table for the purpose of becoming still fatter! (loc. cit., p. 1566.) It is hard to believe that such scientific argument can be produced in a world where millions of people are constantly suffering from want and starvation, in a world which might easily produce an abundance of chewing gum and similar stuffs.

Likewise in 1951 TINBERGEN again wrote: "The performance (of a consummatory act) seems to 'satisfy' the animal, that is to say, to bring about a sudden drop of motivation... LORENZ has pointed out that the end of purposive behaviour is not the attainment of an object or a situation itself, but the performance of the consummatory action... Even psychologists who have watched hundreds of rats running a maze rarely realize that, strictly speaking, it is not the litter or the food the animal is striving towards, but the performance itself of the maternal activities or eating." (loc. cit., pp. 105–106). No further argument was given at this point. No mention was made of TINBERGEN's compatriot PORTIELJE who as long ago as 1938 had recognised that hunting behaviour may originate *either* from a need for food or from a (more or less specific) "urge to hunt" and who thereby recognised the hierarchical organisation of feeding behaviour. Nor was mention made of other authors on this topic, whether dealing with hierarchy, or with motivational studies, or with specific hungers, or with veterinary research on food-intake. No serious argument was put forward by TINBERGEN at this crucial point, nor has such an argument ever been given by LORENZ, as far as this writer knows. This state of affairs is especially surprising, because the dogma according to which an instinct can be satisfied *exclusively* by means of a consummatory *act* has always been precisely the essential point of divergence between ethologists and other workers on instinct on the Continent of Europe, apart from some philosophical framework that may be considered only metaphysical embellishment.

To be sure, nobody will doubt that there do exist *some* instincts which can be satisfied exclusively by the performance of a consummatory act. The copulatory instinct provides a good example, for we know that the presence of sperm, or oestrus, is not required for the excitation of the drive, so there must be another source of endogenous motivation causing threshold fluctuations. In other instincts, however, things are quite different.

As a matter of fact it is fairly easy to prove that LORENZ' and TINBERGEN's statements with regard to feeding behaviour (quoted above) are at least partially wrong. For example, a young cormorant when being fed by man will continue to beg for some time after having swallowed the food and will stop begging apparently as soon as the food has arrived in the digestive area of the stomach. If the young bird is forced to regurgitate its food it will very soon start begging again, so evidently it cannot be satisfied by eating without digesting food. Therefore the young bird's "goal" is not (or not only) eating and swallowing, but (also) alleviating hunger pangs. In other words, superordinate to possible appetites directed toward the performance of eating and swallowing, a top-level appetite directed towards a full stomach has to be postulated. Further, as early as 1934, HAUSMANN proved by means of artificial physiological "leaks" that, in rats, the amount of feeding on carbohydrates depends on actual tissue needs. Similar and other evidence with regard to mammals has been extensively reviewed by YOUNG (1941). Further, as a result of learning experiments in chickens, WOLFE and KAPLON (1941) could separate the rewarding influences exerted by the food itself and by the consummatory activity. Moreover, JANOWITZ and GROSSMAN (1949) have demonstrated that in dogs with esophagostomy and gastric fistula the amount of oral food intake is largely controlled by the amount of intragastric feeding, provided that oral false feeding proceeds at the same time as intragastric feeding. (See also Chapter II, pp. 186–187.) HINDE (1953, pp. 208–209) although unprepared to draw a definite conclusion, has given an analogous argument with regard to the Great Tit (*Parus major* L.). Evidence from animal husbandry referring to cows has been summarised by HANCOCK (1953) as follows: "Despite a statement by JOHNSTONE-WALLACE, based on rather scant observations, to the effect that the time spent grazing was almost constant, even when the available feed varied between 250 and 1000 lbs. per acre, it is now fairly well established that cows graze longer hours when little grass is available to them, either on a per cow or per acre basis or both, than when the pasture is ample in all respects. Thus it was found that cows grazing on a ley with short grass, grazed for more than two hours longer than when grazing on another ley with grass 6–8" long... Cows consumed about one and a half times as much young leafy pasture on a fresh weight basis as stemmier material, although the difference in dry matter intake was negligible... In one series of observations JOHNSTONE-WALLACE and KENNEDY found that, while the dry matter intake fluctuated from 32 to 10 lbs. per cow, the grazing times remained almost constant... The same authors and others also reported that the stage of lactation, individual milk yield and live weight appeared to have no relation to the time cows (within a herd) spent in grazing. However, in a recent New Zealand trial it was found that, in each of four fortnights, there were highly significant correlations between grazing times of individual cows and their theoretical feed requirements for production and maintenance. In this trial twenty animals (ten sets of identical twins) were observed simultaneously for six 24-hours periods in each fortnight. It can perhaps be concluded that within a herd a distinct relationship between grazing time and theoretical feed requirements does exist, but that individual differences in grazing efficiency (feed intake per unit of time) and day-to-day variations in grazing time are of sufficient importance to obscure such relationship unless a great number of cattle are observed several times at close intervals." (Loc. cit., pp. 4, 5 and 6.) For the rest, HANCOCK in his review stresses also that grazing times are longer if the quality of the grass is better (low fibre content), which phenomenon produces an opposite effect as compared to the relationship quoted above. Apparently in this case palatability plays a role. Further, an important point of view is that "cattle, given time, will change their habits to a considerable extent in order to meet changes in their environment". (Loc. cit., p. 11.)

From all this evidence there seems no doubt that, at least in the higher vertebrates, eating, swallowing, hunting and similar activities (perhaps also drinking) are hierarchically *subordinate to the appetite for food* instead of being determined exclusively by the appetites for discharging fixed motor patterns. For the rest it would be incredible, from a general biological point of view, if there were no adaptation at all of the animal's food intake to its physiological needs. One can only wonder therefore, that LORENZ and TINBERGEN have never tried experimentally to check up the validity of their somewhat revolutionary ideas on this point, instead of formulating dogmatic statements such as quoted above.

What has been argued here with regard to food-seeking behaviour, applies mutatis mutandis to several other instincts. From investigations on dominance and submissive behaviour, especially in mammals, we know that the goal of fighting in many species is not so much fighting in itself but rather to establish a social organisation which makes fighting superfluous. Here the goal is not an "object" (as in feeding) but a social "situation". Similarly the goal of pair-forming behaviour in the cormorant is a marital "situation" which makes pair-forming behaviour superfluous. In nesting behaviour on the other hand, the top-level goal is to accomplish an "object" which makes nesting behaviour superfluous. Ultimately, in these instances, it is mainly the presence or absence of an object or situation which satisfies or creates the drive. All these facts have never been taken into consideration in the ethological concept of hierarchy, and it is exactly this state of affairs which has hampered ethologists in recognising the full implications of the principle of hierarchy.

Recently, however, a turning point seems to have been reached as a result of an ingenious investigation in *Salticids* by DREES (1952) and PRECHT (1952). These authors demonstrated the existence of an appetite for food (Hungertrieb) and a sexual appetite (Geschlechtstrieb) together with a "container" (Reservoir) of instinctive energies. The first two appetites may be put on an equal footing with MCDOUGALL's concept of top-level instinct (except for the MCDOUGALL link discussed in Chap. II) whereas the "container" may be regarded about equal to a top-level instinct as conceived by TINBERGEN. Further, DREES and PRECHT showed that various activities (hunting, courtship, nest-building) are all driven by impulses which flow out from this one "container", whereas the release of these activities depends on the strength of the hunger and sexual tendencies. (Terms "impulse" and "tendency" as defined in Chap. II of this paper.) Finally the reloading of the "container" appears to depend on the strength of the hunger and sexual tendencies. In other words the whole system may be characterised as a sort of X-shaped combination of the type of hierarchy represented in Fig. 7 and the type represented in Figs. 2–6 in this paper. This conclusion means that the existence of instincts which cannot be satisfied by the performance of a consummatory act has now also been definitely proved in a non-vertebrate species, and further, it implies that the distinction between "satisfaction" and "abreacting" as made by FREUD and adapted to the field of animal behaviour in Chapter II of this paper, applies also to a non-vertebrate species. (See p. 181.)

Other authors who have definitely broken with the doctrine of the consummatory act are BASTOCK, MORRIS and MOYNIHAN (1953, p. 73). According to them: "It would seem therefore that an adequate explanation of our examples demands some revision of ideas concerning the ways in which drive can be consumed... Our observations make it clear that, in some situations at least,... the postulation of consummatory stimuli seems necessary." Further, MOYNIHAN and HALL (1954, p. 41) conclude that gregarious motivation in the Spice Finch (*Lonchura punctulata*) is consumed by a consummatory situation. One wonders only why these authors present their ideas as a "revision" of ethological theory instead of frankly stating that they are converts to other schools which have always advocated these ideas on exactly the arguments advanced by these authors themselves.

Quite recently two other adherents of the ethological school, Hinde (1954) and Thorpe (1954 b), have also crossed the demarcation line between ethology and other schools by stating that "a lowering of responsiveness is not necessarily due to the performance of an activity" (Hinde p. 47) and "consummatory situations are clearly demonstrated if we analyse carefully the process of, say, the building of a complex domed nest by a bird such as the long-tailed tit." (Thorpe, p. 103). Both authors, however, still maintain that the impulse is only *inhibited* by a consummatory situation, instead of simply and consistently concluding that the impulse is actually *consumed* and that it is *no longer produced* due to the presence of a consummatory object or situation. Neither do these authors consistently conclude that an impulse can be *generated* by the absence of a consummatory object or situation such as Drees and Precht do. All this makes the concept more complicated than need be. The idea of "inhibition by consummation" sounds much like a contradiction in terms. The question: what becomes of the "inhibited" impulse? will require an additional explanation, considering that no displacement nor threshold lowering is observed; on the contrary, the "inhibited" impulse actually appears to have dissolved for ever.

These points are essential in order fully to understand Tinbergen's concept of hierarchy. In his system of presumptions a very sharp distinction is made between appetitive behaviour and consummatory act. In appetitive behaviour the impulse is supposed to be conducted downward from centre to centre, guided by external directing stimuli and *without losing anything of its strength*, until a situation is reached in which one or another IRM is met with and a consummatory act is released. In the consummatory act, on the other hand, the impulse is assumed to be discharged and consumed[1]. It will be clear that this theory *necessarily implies* a hierarchy of innate *directing* mechanisms leading impulses from the higher motivating centres to the centres of consummatory acts, i. e. to the bottom level of hierarchy. But it will be clear too, that this implication *will not hold* if it should be proved that an impulse can be consumed (or satisfied) by the attainment of an object or a situation, instead of being consumed by the performance of a consummatory act, for in that case we need not assume an efferent nervous conducting system in which all impulses necessarily lead up to a consummatory act, and by this Tinbergen's model would lose its inner consistency. Now the experiments on dogs with esophagostomy and gastric fistulae demonstrate that cases do occur in which the impulse is consumed or satisfied at the level of a top centre, and the same applies to nesting behaviour in the cormorant and other instances mentioned in this paper. Such cases prove that an impulse generated in a top-level centre can indeed be satisfied without running down the whole hierarchical system. At least there seems to be sufficient reason to doubt the validity of the assumption according to which an impulse can be discharged and satisfied only by means of a consummatory act, and this conclusion gives a new setting to the problem. Further, HINDE (1953, pp. 190-194) has demonstrated that appetitive behaviour and consummatory act differ only in degree and not absolutely. Moreover, VAN IERSEL (1953, pp. 133-134) found that the performance of appetitive behaviour as well as a consummatory act may cause a drop in motivation. It may be added that TINBERGEN's statement "a peregrine falcon in which the hunting drive becomes active, searches for prey until it is found" (1950, p. 307) is erroneous. If no food at all is found the bird will stop hunting long before it is physically exhausted: the drive becomes "abreacted" without being satisfied, as explained in Chap. II. At least, judging from my experience with cormorants, it seems quite certain that hunting behaviour shows the characteristics of a consummatory act (threshold lowering and nervous exhaustion), and yet *at the same time* hunting may serve as appetitive behaviour in order to satisfy the need for food. This means that hunting, as far as it is generated by a specific impulse for hunting, can be discharged and satisfied only be means of *hunting itself*, whereas hunting as far as it is generated by a need for food can be discharged and satisfied only by *filling the stomach.* Here again we see that the essential feature of hierarchy is a hierarchy of *goals* instead of being a rather simple causal switch-board hierarchy for conducting impulses to their motor outlets, as conceived by TINBERGEN.

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[1] The consummatory act seems to be the corner-stone of Tinbergen's theoretical system. For example the existence of a social instinct is rejected because there are no specific social consummatory acts, although there is social appetitive behaviour.

In other words, in TINBERGEN's concept the *ways* conducting impulses downward are supposed to be hierarchically organised but the *goals*, i. e. the consummatory acts, are definitely *not.* In this respect he has maintained the original rejection of hierarchy as formulated by LORENZ (1935) and cited earlier in this chapter, to quote: "In animals, or at least in birds, I cannot see any possibility of distinguishing between high order instincts and low order instincts as has been done by McDOUGALL." In McDOUGALL's doctrine the essential feature of instinct is its goal and in TINBERGEN's doctrine no other goals are recognised than bottom-level goals. One might say, therefore, that until now, TINBERGEN has continued to deny the very essence of the idea of hierarchy of instincts.

In KORTLANDT's concept, on the contrary, *not only the ways* conducting impulses downward, but *also the goals* (i. e. the acts and situations which may extinguish an impulse) are assumed to be hierarchically organised. In other words, in this concept it is not necessarily implied that an impulse generated in a top-level centre will run through the whole hierarchical system until the bottom: the impulse may be satisfied half-way through the system (as in cases in which a cormorant is "hunting" dead fish and swallows them without making munching movements) or even at the top (as in intra-gastric feeding of dogs, or if a cormorant stops building after having stolen a nest). The examples mentioned here, and many similar ones, seem to be inconsistent with Tinbergen's switch-board model, unless supplementary hypotheses are postulated. Instead of more theorising, it may be better to drop the idea according to which satisfaction can be attained only by a consummatory act and not by an object or a situation.

Other points of divergence

Further, in Tinbergen's concept, all centres higher than those at the level of the consummatory act are considered to be only switches and generators of nervous energy, without attributing to them any co-ordinative or integrative effect. In this respect too, the higher levels are assumed to be of an entirely different nature as compared to the bottom one. (See the distinction beween "inhibitive" and "coordinative" interrelations made on the right of Fig. 98 on p. 125 in Tinbergen's book.) In Kortlandt's concept on the other hand, *all* centres ("appetites") are assumed to act as co-ordinating and integrating agents. As put forward in Chap. II, pp. 190–192, this assumption is founded, inter alia, upon the fact that the highest activated appetite appears to promote normal variability of behaviour at a level just below it, but appears to suppress the normal variability of behaviour at the lower levels. In other words, Kortlandt's findings on this point harmonise very well with neurophysiological evidence gathered by Weiss, and by Hess, Brügger, et al., whereas Tinbergen's concept diverges from it and leads to the assumption of two different types of hierarchy, viz. an instinctual one characterised by mutual inhibition, and a neurophysiological one, characterised by mutual integration. (See Fig. 98 in Tinbergen's book: above and below the thick black line respectively.) For the rest, there is no need to state that in many cases integration as conceived by Kortlandt will be actually identical to inhibition as conceived by Tinbergen, for the integrational process may consist of a choice between different means as well as a combination of different means leading to a goal. In such cases there exists no real distinction between these aspects.

A similar divergence between the two authors is found at the afferent side of the problem. According to Tinbergen the IRM of a superordinate instinct is always *less* specialised (i. e. *less* selective) than the IRM of a subordinate instinct. According to Kortlandt on the contrary, in his terminology, a superordinate appetite is as a rule *more* selective and can be satisfied only by a *more* specialised object or situation in comparison with a subordinate appetite of the same hierarchical system.

At first glance this antithesis will seem rather surprising and, moreover, easy to solve by means of fact-finding research. On closer examination, however, the divergence will be found to be highly interwoven with general theory and for the rest it will appear to be due to a terminological inconsistency on TINBERGEN's part. In order to understand this point, one must again bear in mind that in ethological theory a very sharp distinction is made between "appetitive behaviour" and "consummatory act". In a *non-hierarchical* system this distinction can quite easily be understood. In this case appetitive behaviour is characterised by the following features: (1) it is highly adaptive and plastic according to environmental circumstances, (2) it is guided by innate *directing* mechanisms, (3) its does not contribute to the satisfaction of the animal's need. A consummatory act, on the other hand, is characterised as follows: (1) it is entirely rigid, (2) it is released by an innate *releasing* mechanism, (3) it brings about satisfaction. In a *hierarchical* system, however, the distinction between appetitive behaviour and consummatory act is less comprehensible. In this case, according to TINBERGEN, appetitive behaviour is characterised by the following features: (1) as shown above, (2) at the switch-points (or centres) the choice between different courses of appetitive behaviour is taken to be guided by innate *releasing* mechanisms, (3) as shown above. The features of consummatory acts in a hierarchical system are the same as above, because they are taken not to be arranged hierarchically[1].

Owing to this terminological inconsistency, TINBERGEN is lead to assume a hierarchy of IRM's in which, naturally, the IRM of a superordinate instinct is always *less* specialised and *less* selective than the IRM's of the instincts subordinate to it. If, however, the technical meaning of the term IRM is restricted again to its original connotation in ethology, namely that the IRM is the mechanism by means of which the process of discharge and satisfaction is released, all IRM's in TINBERGEN's scheme appear to be arranged at bottom-level and nothing of their hierarchy is left. In that case the ethological postulate according to which discharge and satisfaction *occur always at bottom level* comes to light again.

In KORTLANDT's conception on the other hand, the goals (i. e. acts as well as objects and situations which cause discharge and satisfaction) are taken to be arranged hierarchically, and consequently in most (but not all) cases the object or situation required to satisfy a superior appetite is a coalescence or fusion of the objects and situations required for satisfying the subordinate appetites. This implies that in most cases (but not always) the object or situation required to satisfy a superordinate appetite will be *more* specialised than those required to satisfy a lower appetite. For example, quivering movements can be made with nearly any small object, inserting can be accomplished only by using long, thin and stiff objects, and inhabiting a nest is possible only by owning one. In order to prevent confusion KORTLANDT did not use the term IRM at all, but apart from this, it will be clear that essentially a true hierarchy of IRM's was postulated, whereas in TINBERGEN's conception there is something like a hierarchy, but not of IRM's. Consequently KORTLANDT's conception can explain increasing selectivity during maturation, whereas TINBERGEN's cannot. As a matter of fact, in TINBERGEN's expositions the ontogeny and maturation of hierarchical systems have not been dealt with at all.

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[1] In TINBERGEN's considerations one searches in vain for an argument explaining why *hierarchical* appetitive behaviour is supposed to be guided by *releasing* mechanisms, whereas *non-hierarchical* appetitive behaviour is supposed to be guided by *directing* mechanisms. Perhaps this inconsistency can be explained by historical circumstances. As expounded earlier in this paper, BAERENDS recognised in the digger wasp a true hierarchy of *internal* drives, i.e. a hierarchy of appetites requiring satisfaction. In the framework of his findings the supposition of a hierarchy of IRM's could be justified. TINBERGEN afterwards extended BAERENDS' conception to a hierarchy of *external* factors. Presumably he did not realise that by doing so, the hierarchy of IRM's became transformed into a hierarchy of innate *directing* mechanisms or at least an ambiguous hierarchy which cannot be considered a true hierarchy at all.

Convergent evidence of similar tenor pointing to a higher selectivity and specialisation at the higher levels can be found in the neurophysiological investigations of HESS, BRÜGGER, et al. For the rest, it will be remembered that the ideas advocated here have been largely derived from FREUD on the one hand and PORTIELJE on the other hand. Moreover, the validity of these ideas has been proved in human psychotherapy.

An attempt at reconciliation

There is one point with regard to which the gap between the controversial views discussed here may be fairly easily bridged by creating terminological clarity. This point may be illustrated by means of some simplified examples serving as models of thought. Let us suppose that an animal employs two consummatory activities, called A and B, the performing of which has appeared to be dependent upon one or another common causal factor. Now with regard to the type of hierarchical interrelation there exist three basic possibilities:

1. Let us assume that performing A leads to threshold heightening in A but not in B, and moreover that performing B leads to threshold heightening in B but not in A. In this case apparently A and B are *not* dependent upon a common source of *nervous* energy and therefore the term hierarchy should *not* be used at all even in cases in which A and B are dependent upon a common hormone or a common component in their releasing stimuli. In other words, if this proposal finds acceptance, the term hierarchy will be restricted to cases in which evidence has been found of a *common charging* or *loading* factor, and the term will be excluded in cases in which only common *initiating*, *augmenting* and *trigger* factors have been found. In a terminology referring to purposiveness one may state that A and B have no common goal, because satisfying A does not satisfy B and vice versa. (See Fig. 9a.) An example of this type of interrelation is obtained if, in the cormorant, advertising display is called A and copulation is called B.

2. Now take the case that performing A leads to threshold heightening in A as well as in B, both in the same degree, and, moreover, that performing B leads to threshold heightening in B as well as in A, both in the same degree. In this case, apparently, A and B are both dependent upon *one single* source of nervous energy[1]. Or in other words, changes in

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[1] In this context, displacement phenomena are left out of account.

internal reactive preparedness for A and B appear to be entirely due to one single charging factor. Therefore in this case *only one single "instinct"* (not a hierarchy of instincts) should be postulated. In addition to this, however, a *hierarchy of motor outlets* subordinate to this instinct should be postulated. In a terminology referring to purposiveness one will postulate only one goal but two means of satisfaction. In the cormorant this type of organisation is approximated if wing-flapping is called A and gargling is called B, provided that all the remainder of the male pair-forming behaviour is left out of account. Another example is the "container" with its subordinated mechanisms as described by Drees, provided that the superordinate feeding and sexual instincts are left out of account. Such a scheme of this type of organisation is shown in Fig. 9b.

3. Put the case that performing A appears to lead to a well-marked threshold heightening in A but no threshold heightening in B, whereas performing B leads to a well-marked threshold heightening in *both* A and B. In this case it will be clear that there must be at least *two* sources of nervous energy, one of which is charging only A and one of which is charging *both* A and B. This means that in this case, postulating *a true hierarchy of "instincts"* is fully justified. In a terminology referring to purposiveness one might state that one goal is to satisfy A and another goal is to satisfy the common need underlying A and B. Such a scheme has been given in Fig. 9c.

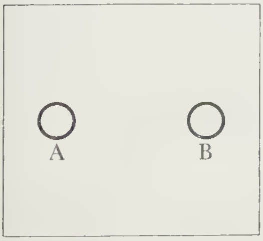

Fig. 9a

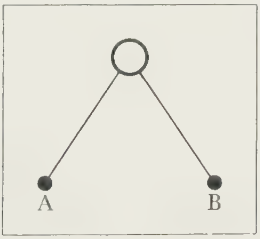

Fig. 9b

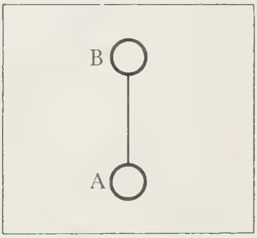

Fig. 9c

An interesting point in this type of organisation is that, as a rule, (and perhaps always) A seems to serve as appetitive behaviour in the service of B. It looks as if Nature mistrusted appetitive behaviour and therefore has added to it some interim reward. A typical example of this type of organisation in the cormorant is found in copulatory behaviour, in which A is represented by mounting and B by coition or ejaculation. Other examples are: hunting (A) – eating (B), and quivering (A) – inserting (B). The important implication of this point with regard to general theory will be considered in Chapter IV, § 4, pp. 261–262.

In addition to the three basic types described above, other types might occur, theoretically speaking. (E. g.: Performing A causes threshold heightening in B but not in A, performing B causes threshold heightening in A but not in B.) Up to now, however, actual research has found no evidence pointing to the existence of these other theoretical types of hierarchical interrelations. This may offer a starting point for neurophysiological considerations on hierarchy.

For the sake of completeness it should be added that in this review only the principle of hierarchy has been considered. Other principles of interaction which have nothing to do with hierarchy (e. g. inhibition, priming, displacement, etc.) have been left out of account. Further, it must be stressed that the three cases described above refer only to those instances in which there is agreement in principle but divergence in terminology among different authors, i. e. instances in which the impulse is supposed to be satisfied by means of a consummatory act.

The proposal just made in order to create terminological unity and clarity may be considered in several respects to be a suggestion to return to the stricter concept of hierarchy as defined by Baerends, in comparison with the broader concepts that have come into vogue during recent years. In this proposal an attempt has been made to do justice to what might be called perhaps the most essential achievement of the ethological school of investigators, namely the discovery of instinct-specific endogenous stimulus production and nervous exhaustion. The hope may be expressed therefore that this proposal will be accepted as a contribution to bridge the conceptual divergence between those investigators who are thinking in "causes" and those who are thinking in "goals". In this way at least a partial unification may be gained by linking up common speech to concepts referring to directiveness, and to results of neurophysiology. Ultimately the concepts of "cause" and "goal" are not irreconcilable, for a "cause" is the cause of a beginning and a "goal" is the cause of an ending. Moreover, by eliminating terminological obstacles, full attention can be concentrated upon the core of the existing controversy: the question whether satisfaction can be gained only by a consummatory act, or also by a consummatory object or situation, and further, the question whether there is, or is not, a difference between satisfaction and abreacting.

There is good hope that in future a rapprochement on these points will be possible, in view of the revisions in ethological thinking quoted on pp. 207–208. The same hope may be justified by the fact that recently Tinbergen (1954) has acknowledged the contributions made by "non-ethological" workers with regard to "ethological" problems, including the problem of hierarchy. Anybody who has ever experienced the depth of the lack of mutual understanding among students of behaviour of different origin will realise the prospective significance of these events.

Attitudes and backgrounds

Having arrived at the end of this Chapter,the reader may wonder why a paper like this has not been written by a member of the ethological school. Chronologically speaking, ethology is the youngest of three or four or five main trends of thought leading to the idea of a hierarchical organisation of instincts. The idea of hierarchy appears to have had a very long history indeed, in animal psychology as well as in human psychology, psychiatry and neurology. At first glance, therefore, it may seem rather surprising that ethologists have entirely neglected this existing knowledge, and that some of them have even explicitly claimed hierarchy to be exclusively a discovery of their own school. One would have expected on the contrary that ethologists on their side would have made an attempt to compare their conceptions with previous ones in order to provoke a scientific discussion that might clarify the whole problem. On closer examination, however, this state of affairs will appear to be less surprising.

The adherents of ethology usually claim that their science is a new one, or that the ethological way of approach is the only scientific one in this field (TINBERGEN 1951, pp. V–6; LORENZ 1952). Of course such a statement is somewhat exaggerated. New sciences are not founded by christening a group of workers in an existing field of research. As a matter of fact, ethology is not so much a separate science as a state of mind, a scientific reform movement, a body of scientists who are characterised by an entirely praiseworthy predilection for field-work and by an equally praiseworthy zeal to do actual research. Given these characteristics, it is quite natural that such investigators are handicapped by a lack of time and interest to read all the existing literature. It is quite natural too from a human point of view, that this regrettable state of affairs has been gradually camouflaged by the creation of the fiction that ethology is an entirely new science instead of being only a renewed approach to old problems. For by this fiction, these workers are relieved of the arduous duty of reading existing literature, of understanding previous authors and of integrating their own findings with existing knowledge. Such a fiction creates a climate in which an unpleasant duty can be dismissed as superfluous, or even invested with an armchair-and-white-collar-taboo. Mental processes of this type occur, in scientists as well as in ordinary citizens, as we know from psychology and sociology. As a rule these processes work subconsciously, for behind the barrier created in this way, the individual as well as the group continue to feel safe as long as the illusion can be maintained. Perhaps this paper, by showing the actual scientific situation with regard to the problem of hierarchy, will contribute a little toward destroying this illusion.

It is beyond the scope of this paper to give a complete and scientific argument on the assertion expressed above. Some comment, however, may be useful in order to indicate that there do exist solid grounds for this view.

As an example, TINBERGEN's book "The Study of Instinct" (1951) may be taken. The aim of this book is stated to be, among other things, the following: "First, it is intended to call the attention of Anglo-American workers to research done on the European continent." (Loc. cit., p. V.) Nevertheless in this book no mention at all is made of two important books dealing mainly with the concept of instinct and written by TINBERGEN's compatriots BIERENS DE HAAN (1940, 478 pages) and PORTIELJE (4th edition 1948, 535 pages). Of both authors only some minor papers of little importance have been quoted. No reference at all is made to any book or paper written by BUYTENDIJK (Holland), DE MONTPELLIER (Belgium), HEDIGER (Switzerland), FISCHEL, B. SCHMID (Germany) and other prominent continental workers who belong to other schools than the ethological one. The second aim of TINBERGEN's book is stated to be: "to elucidate the hierarchical nature of the system of causal relations, and to stress the paramount importance of recognizing the different levels of integration". (Loc. cit., p. V.) Actually, W. R. HESS et al. and P. WEISS are the only non-ethological authors mentioned by TINBERGEN in connection with hierarchy and integrational levels.

Apart from TINBERGEN's stated aim to review European literature, it is rather surprising to find that in a book dealing with instinct, scant attention has been paid to leading American contributors in this field. For example, ALLEE, HEBB, HULL, MASLOW, MASSERMAN, RIESS, SCHNEIRLA, SCOTT and YERKES have not been mentioned at all. With regard to TOLMAN, no details are given other than that his main book is dedicated to M. N. A. (*Mus norvegicus albinus*). A further feature is that TINBERGEN has occupied himself very little or not at all with historical people who exerted great influence and shaped the notion of instinct before the rise of ethology, such as ALVERDES, BRUN, GROOS, KATZ, W. KÖHLER, LLOYD MORGAN, McDOUGALL, PAVLOV, VON UEXKÜLL and WATSON, not to speak of those investigators who studied instinct only in man, such as FREUD, JUNG, and VON MONAKOW. Thus the wrong impression is given that the study of instinct is a special achievement of ethology. To be sure, TINBERGEN's book is very instructive indeed, not only for its contents but also for what is not mentioned. In this respect the present situation in ethology shows much resemblance to that in psychoanalysis some decades ago.

Another feature which is found in many ethologists is a curious avoidance of all the more anthropomorphic beings such as mammals (especially domesticated ones) and man. Among 130 illustrations in TINBERGEN's book only one (No. 116) concerns mammalian behaviour and this one appears to represent precisely a hare fleeing from man! (In continental Europe the hare has the same symbolic meaning as the rabbit in England.) Of the two illustrations concerning human behaviour (No. 76 and No. 130) at least one is intended to be nothing other than a zoomorphic joke of the same type as the anthropomorphic jokes on animals often cracked by humorists. One is reminded of the cartoons of WALT DISNEY who is as gifted an observer of animals as is TINBERGEN, but in whose films man appears either as a beast or as an artistic failure but never as a beauty.

Given this state of affairs it is no wonder that TINBERGEN accounts for his neglect of the vast amount of work done by American physiological psychologists by stating that these investigators are characterised by "a preoccupation with what is often called prehuman behaviour in mammals". (Loc. cit., p. 6.) When reading such statements one cannot help pondering on a possible psychological relation between (scientific) psychophobia, anthropophobia and mammalophobia. C'est le ton qui fait la musique. Similar meditations are elicited when reading in TINBERGEN's final chapter (entitled "The Ethological Study of Man"): "Human ethology is still in its infancy. Yet the evidence is already much too voluminous to be covered here", which statement is followed by a number of assertions such as "Every individual among us knows", "Everyone knows", "Although no well-planned experiments have been carried out, there is evidence", "Reliable observers have told me", and so on (pp. 207–210). Facts which apply exclusively to twentieth century western peoples are offered by TINBERGEN as arguments to prove the innateness of certain forms of behaviour in man (p. 209). The difficulty of studying innateness in man is attributed to the variability of human behaviour (p. 210), although actually the difficulty is found in man's biological inability to escape from culture and it is precisely variability which offers still further possibilities. No mention at all is made of such investigations as have been carried out by BENEDICT, MEAD, and others, nor of any research on twins. This way of dealing with man provides a striking contrast indeed with most textbooks of general psychology in which due attention is usually paid to findings of animal psychology including those achieved by the ethological school.

Finally, TINBERGEN seems to be unaware of the true nature of human psychology, for in his account this science is more or less equivalent to the study of "subjective", i. e. conscious, or introspective phenomena (pp. 4–6, pp. 205–206). This characterisation would have been partly correct sixty years ago, before FREUD, ADLER and JUNG. Contemporary human psychology, however, might be defined more appropriately (although with a little bit of exaggeration) as the study of *un*conscious phenomena in man, or the study of the discrepancy between conscious rationalisation and unconscious actual behaviour, or something like that. Hence, in this Chapter too, where we are dealing with the psychology of ethologists from a point of view of attitudes, the question whether these attitudes are conscious or not, has been consistently left out of account.

The distinction between European and American psychology as made by TINBERGEN (p. 6) is also out of date. Pre-war migrations of refugees, war requirements and post-war scientific contacts have blurred geographical boundaries between academic schools. Nowadays all essential divergencies cross the Atlantic. (See e. g. DENNIS et al. 1947, ROHRER et al. 1951.) Perhaps the chief remaining difference is that American psychology is more aware of social and sociological points of view whereas European psychology has still preserved much of its original individualistic orientation. This difference cannot be called an essential one. Further, European psychology has gradually lost its originally predominant character of a "Geisteswissenschaft" and has become more like a social science. In this connection one should not overlook, also, that human psychology in the past twenty years has advanced and changed more than animal psychology (including ethology). For the rest it must be remembered that the objectivist approach was applied first in human psychology in the nineteenth century (e. g. by EBBINGHAUS and WUNDT) and was introduced afterwards in animal psychology as a reaction against Darwinian animal psychology (e. g. ROMANES). Actually, psychology has always been more sensitive to methodological problems than any other science.

In order to prevent misunderstanding, it should be added that the above short review of prevailing attitudes in contemporary ethology is not intended to be a criticism of ethological findings but an analysis of the attitudes of mind which have hampered ethologists from realising the full bearing of their findings on hierarchy. For the purpose of this analysis TINBERGEN has been taken as an example in order to demonstrate certain tendencies which are relevant to explain the present state of affairs. Similar tendencies can easily be demonstrated in the writings of LORENZ and other members of the ethological school. In the scope of this paper it would be impossible to give a complete account. It will therefore have to suffice to give only one single further example to demonstrate how ethologists have failed to recognise an important aspect of hierarchy. We allude to the history of ideas on the process which is called "object-choosing" and "fixation" in psychoanalysis, or "imprinting" in ethology.

This process seems to have been described first in chickens by SPALDING (1873, pp. 287–289; reprinted 1902 and 1954, pp. 6–8). At that time these experiments aroused considerable interest. Consequently similar experiments were undertaken and the results published by famous men such as PREYER, the founder of child psychology (1884), EIMER, the father of the concept of orthogenesis (1890), WESLEY MILLS (1895), and LLOYD MORGAN, the founder of twentieth century animal psychology. (Full quotations in LLOYD MORGAN, 1896, pp. 30–36, and BREED, 1911.) Further, with regard to birds, imprinting was described in ostriches by HUDSON (1892; ed. 1923, pp. 84–85), in geese by HEINROTH (1910, pp. 633–634) and in doves by CRAIG (1914). In mammals, especially hoofed animals, the same phenomenon has been described by BAIN (quoted by SPALDING 1873, p. 283), HUDSON (1892; ed. 1923, pp. 105–106), WILLIAM JAMES (quoted by VON HATTINGBERG 1921, p. 408), MCDOUGALL (1923, pp. 111–112) and HECK (1930, pp. 97–99). The fact that lambs are very susceptible to imprinting during the first two days or so of life has always been widely known, for imprinted sheep have little economic value and therefore sheep-farmers have always given attention to this phenomenon. Finally, with regard to insects, imprinting or something of a similar nature has been described by the ant-investigator and psychoanalyst BRUN (1920, pp. 101–109) and by THORPE (1928, pp. 630–631).

All these sources were fairly common knowledge among (non-ethological) animal psychologists in the twenties and thirties and they have often been quoted in common text-books (e.g. BIERENS DE HAAN 1940) and scientific papers (e.g. DENNIS 1941). Moreover, these sources were also discovered by psychoanalysts and aroused much interest in their circles, for these facts seemed to prove a biological basis underlying similar phenomena in man as described by FREUD and other psychiatrists. Consequently the classic authors mentioned above have often been quoted by psychoanalysts, in scientific papers (VON HATTINGBERG 1921, p. 408; BRUN 1926, p. 6) as well as in elementary text-books of psychoanalysis (e. g. WESTERMAN HOLSTIJN 1936, BRUN 1946). In this connection not only the concept of "object-choosing" in psychoanalysis should be mentioned, but also the concept of "key experience" (Schlüsselerlebnis) current in classical psychiatry with regard to progressive delusions. The last mentioned concept seems to have been introduced by E. KRETSCHMER (1918, pp. 20–22, 128, 138) to whom we owe several very important contributions on the border-line between biology and psychiatry.

When LORENZ (1935) described his findings on imprinting in birds he attributed to HEINROTH (1910) the discovery of the phenomenon as well as the coining of the German term "Prägung". None of the other earlier authors quoted above were mentioned in his account. With regard to mammals LORENZ stated: "Imprinting of object finds no counterpart in the psychology of any other animals, especially mammals. Certain analogies to pathological fixations to instinctive objects in human mental life, however, can be mentioned." (Translated from loc. cit., p. 166.) "In human psychopathology there are cases in which an irreversible fixation of the object of certain instinctive activities has been observed, which purely symptomatologically present a picture absolutely identical to that which we know in birds." (Idem, p. 379.) No further comments concerning these items were made. Considering that LORENZ is a medical doctor and was living at that time near Vienna, we may assume that these statements refer to psychoanalytical concepts, but neither FREUD nor psychoanalysis in general were explicitly mentioned. In those days, books by Jewish authors were being publicly burned in Germany.

In subsequent papers dealing with imprinting LORENZ continued to mention HEINROTH as the sole discoverer of the process of imprinting but claimed the technical term "Prägung" to be his own invention. (E. g. 1937, p. 299.) Allusions to psychoanalytical knowledge of imprinting phenomena have never been made anymore, not even in post-war papers. Other adherents of the ethological school went still further by explicitly attributing the discovery of imprinting exclusively to LORENZ, thereby neglecting HEINROTH's part. (E. g. TINBERGEN 1951, p. 150.) Thus the isolation of ethological thinking on imprinting increased step by step.

Because of this course of events, ethologists until now have remained unaware of the essential relationship between imprinting and hierarchy, which relationship had been discovered by FREUD some fifty years ago. As explained in Chap. I, according to psychoanalytical theory, object-choosing proceeds mainly at the bottom-level of the hierarchical system at the onset of ontogenetical development of partial instincts. In this respect there is no essential distinction between object-choosing as conceived by FREUD and other conditioning processes. The essential feature in psychoanalytical theory, however, is that (owing to ascending maturation and integration) the characteristics of the objects toward which the bottom-level instincts have become conditioned are *subsequently taken over* by the next-higher-level instincts and largely constitute the characteristics of the objects toward which these instincts appear to be directed as soon as they mature. This process is conceived to continue until the top level is reached. (See also Chap. I, p. 159, Chap. II, p. 195 and Chap. IV, § 2, pp. 242–244.)

Now we have seen in the beginning of this Chapter (p. 197–198) that the idea of hierarchy was originally rejected by LORENZ somewhat dogmatically. Consequently the explanation offered by FREUD with regard to imprinting phenomena could be of no use to LORENZ, and consequently he was obliged to postulate that the age of imprinting of a particular instinct has nothing to do with the age of maturation of that instinct (1935, pp. 167–172). In other words, imprinting was conceived to be something like conditioning without a drive and without a reward. A further consequence was that LORENZ was unable to explain the changes in the optimal sign stimulus which proceed during the intermediary period between imprinting and maturation of the imprinted instinct. Psychoanalysts on the other hand do explain these changes by assuming that the characteristics of objects of more than one instinct are amalgamated together. Consequently LORENZ was obliged to withhold any explanation for what he called "the complete incalculability of falling in love" in a jackdaw which is fixated to man. He could merely state: "A whole series of highly interesting questions are still waiting for an answer here." (Loc. cit., p. 172.) Not a word was said on the fact that psychoanalysts do claim they can explain all these highly interesting questions, at least in principle, by calling upon their developmental theories. One may take such claims for what they are worth but this is no reason why their merits should not be considered.

In good earnest, these matters must be taken seriously. Whereas scientific achievements of mankind are great, individual human lives are short; therefore nobody can afford to start again from the beginning by neglecting existing knowledge. Self-made sciences are as impossible as self-made scientists. Further, any artificial barrier between branches of science, or between groupings of scientists will tend to hamper or cut off existing possibilities of scientific contacts and teamwork. Anybody who has ever been active in more than one branch of science will be in a position to confirm this point. The history of science is full of warning examples of this. Some decades ago when the study of animal behaviour was still neglected by biologically trained workers, there was the case of a psychologist who wanted to study the behaviour of a "low animal", and for that purpose used a hen! At the present time, however, similar mistakes in the reverse direction may easily be made (and indeed, have been made) by ethologists.

This regrettable state of affairs is even symbolised in the term "ethology" as opposed to "psychology", for this denomination is a verbal magic intended to create a barrier that actually does not exist. The same applies to the argument sometimes used by ethologists according to which psychology is the science of the psyche, mind, soul, or spirit, thereby implying that psychology should restrict itself to psychic or mental phenomena, not to speak of "psychical" phenomena. It is especially surprising to find this argument advanced by "etho-logists" who, according to all current dictionaries (Larousse, Oxford, Webster, etc.), are engaged in "the science of ethics, morals and education". By such verbal magic one might even try to convert an electromotor into a thing that moves amber (Greek: electron). Nevertheless the electromotor would simply continue to be what it is. Likewise psychology. And so ethology will continue to be a special band of zoologists who prefer to work in the open air.

Therefore, in this paper, psychology (or, more precisely, *psychobiology*) is conceived as one single all-embracing science, the science of behaviour, covering human as well as animal behaviour, conscious as well as unconscious, and healthy as well as diseased. In other words, the scope of this science is defined by its object (behaviour), not by its techniques (observation or introspection), nor by its educative and social backgrounds (zoology, medicine, anthropology, sociology, pedagogics, or even philosophy). This wider outlook is the only way to ensure that the study of animal behaviour will profit by the achievements of other sciences, and, moreover, it is the only way to ensure that other sciences will give due attention to the results obtained by the study of animal behaviour. Nobody will doubt it is mainly due to ethologists that the study of animal behaviour has now become fairly generally acknowledged to be a scientific occupation, but nobody can expect that the science of animal behaviour will be accorded the full status and recognition it deserves if it is not released from its isolation.

This point of view is especially cogent at this moment, for there is an imminent danger of a new secession in the field of our science, due to the recent development of experimental animal psychiatry and kindred fields of research (experimental psychoses and neuroses, psychosomatics, etc.). This new development threatens especially zoologists and zoological physiologists with being cut off from a field of research in which they might be able to play a very important part, but which field at present seems to be studied to a large (and perhaps increasing) extent by medical men, to a less extent by psychologists, and hardly at all by zoologists. It would be a surprising situation indeed if, in the future, the steadily increasing co-operation of medical and non-medical human psychology should be hindered by an increasing splintering of the study of animal behaviour into a number of isolated branches of research. At present the study of animal behaviour is more flourishing than ever, due to the rise of ethology, but at the same time it is the more threatened by disintegration, which is also due to the rise of ethology. In the case of ethology the merits of isolation have been sufficiently proved by a wealth of scientific advances, but isolated development, if not followed by ascending integration, will fail its biological purpose.

IV. PROSPECTS FOR FUTURE RESEARCH ON HIERARCHY

Biological significance of hierarchy rather enigmatic

In the foregoing Chapters we have found many points of convergence in the ideas on hierarchy developed by medical psychologists, child psychologists and animal psychologists of divergent origin. Nevertheless we cannot yet say that the problem of hierarchy in instincts has been well mapped. Some main points have been explored but between them there still remain many white spots on the map. We have obtained a general framework but not yet an entire network in which all psychologists of any descent can be secured.

Therefore, in this Chapter, an attempt will be made to localise some of these white spots. We will try to find out which points deserve special attention in the course of future investigations. It is only by actual research that the remaining gaps in our knowledge of hierarchy can be closed.

So far, in this paper, next to nothing has been said on the biological significance, or teleological efficiency, or survival value of a hierarchical organisation of instincts. In existing literature also, relatively little attention has been paid to this aspect of the problem. There has been much interest in the question *how* hierarchy works but, generally speaking, most authors have passed over the question *why* it works as it does. This is a curious feature. No true biologist will ever have full confidence in the causal explanation of a biological mechanism if he cannot find out its biological "purpose". With regard to the hierarchy of instincts this aspect is indeed rather enigmatic. Why should a predatory animal have a specific drive, or urge, or appetite for hunting if it already has a superordinate drive, or urge, or appetite for food? Why should a male bird continue to perform some building activities if its nest is already finished? Why should normal development and maturation proceed by ascending stages, followed by integration?

A closer consideration of these and similar questions will reveal several obscure points in the theory of hierarchy. One might even say that the biological (or teleological) value of hierarchy is precisely the central point at which all uncertainties concerning the working mechanism of hierarchy come together, for one first has to know fully how it works before one is able to state why it works as it does. Therefore the question of the biological meaning of hierarchy will be chosen as a suitable starting point.

§ 1. THE FORMATIVE FUNCTION OF HIERARCHY

Biological value of "play" according to Groos

In chronological order the first, and perhaps also the most important contribution to this problem was made before the actual discovery of hierarchy itself, viz. by Groos (1896, 1930) in his theory on the survival value of play. According to his ideas, young animals play in order to to train themselves and to exercise their motor abilities before actual cases of emergency require full proficiency. In his account "animals do not play because they are young, but they are young because they need to play". (Freely translated.) During infancy and youth and while protected by their parents, young animals are able to find harmless occasions in which their motor abilities can be exercised and prepared for the requirements of later life.

This plausible and attractive theory may seem to provide a serviceable explanation for many features of hierarchically organised behaviour. Firstly, it becomes clear why ontogenetic development of behaviour as a rule proceeds in ascending stages: apparently the lower levels can be exercised in more widely varying circumstances while they are detached from vital needs, functioning independently of each other and of the higher levels. In this way a teleological explanation might be achieved also for the observed fact that, during ontogeny, normal variability of behaviour is promoted at a level just below the highest active tendency but suppressed at lower levels. (See Chap. II, p. 191, and Chap. IV, § 3, p. 253.) Secondly, this theory might explain why, during ontogeny, the IRM of a higher instinct (or "appetite") appears largely to be built up of the composing parts of the IRM's of the lower instincts (or "appetites") as stated in Chaps. I-III. Apparently the biological value of infantile learning as postulated by GROOS involves not only the motor aspect but *also the sensory aspect* of behaviour.

Scarcity of evidence on GROOS' *theory*

If a theory looks plausible and attractive this need not necessarily imply that it is right. Curiously, however, little actual research has been done in order to prove or disprove GROOS' theory. KUO's well known experiments on hunting behaviour in kittens (1931, 1938) have provided good evidence on the sensory aspect of the problem but on the motor aspect his information is not conclusive. SUMNER (1934), however, when experimenting on the ontogeny of hunting behaviour in owls and eagles, definitely proved the correctness of GROOS' ideas (loc. cit., pp. 344-345) and concluded: "It is evident that the impulse to capture and kill prey is present at first in a markedly undeveloped state. The slowly developing ability to handle live prey which was manifested by my young raptorial birds was undoubtedly a result of learning. Given an instinctive curiosity which impels the animal to follow moving objects, plus an appetite adapted to a diet of flesh, the rest naturally follows." (loc. cit., p. 356). In this last sentence a valuable suggestion is also found with regard to the biological function of hierarchy. (We will return to this point in § 4, p. 261.) For the rest, however, SUMNER's descriptions are not quite consistent with those given by L. TINBERGEN (1935), and further, the number of birds that were investigated by him was rather small. From other sources BEACH (1945), without explicitly mentioning GROOS' theory, concludes that the beneficial effects of juvenile practice upon adult performance are plausible, but not proved.

A similar scarcity of evidence is found with regard to the question whether practice can improve locomotory co-ordination. According to experiments made by SPALDING (1873) and GROHMANN (1938) the improvement in flying abilities observed in young birds after fledging should be ascribed to neural maturation. According to experiments and other data in cormorants, however, this improvement in flying abilities must be ascribed largely to a special type of learning, called *flash-learning*, which may be considered the analogon on the motor side of behaviour, as compared to what, on the sensory side of behaviour, is usually called imprinting (KORTLANDT 1940 b, p. 413 and unpublished data). Further, DENNIS (1941, pp. 344-345) found in buzzards that "the attainment of adult (flying) skill required a considerable amount of learning". Perhaps both types of development may occur in different species of birds. It would be interesting to correlate such differences with the presence or absence of a special appetite for flying[1].

With regard to mammals there is a fair amount of material, embracing the sensory as well as the motor aspect of GROOS' theory and referring to rats, chimpanzees, and man. (See a. o. BEACH 1945; GESELL 1954; NISSEN, CHOW and SEMMES 1951; KAGAN and BEACH 1953; MARX 1950; RIESEN 1947; RIESEN and KINDER 1952; RIESS, quoted in LEHRMAN 1953, p. 342, and SCHNEIRLA 1952, p. 578; THOMPSON and HERON 1954.) From this material it appears that GROOS' ideas were partially right, partially wrong, and for the rest too simplified in these matters. A quotation from RIESEN (1947, p. 108) may illustrate this point: "The comparative data conform to the generally recognized principle that organisms whose potential adaptations to the environment are most complex, i. e. those that show the greatest intelligence at maturity, also require the longest period of development. This has generally been regarded as a period of maturation. The clinical and experimental data discussed here, however, show that this long period is also essential for the organization of perceptual processes through learning."

But why acquired by play instead of by innate maturation?

From the evidence quoted above one may safely assume that there is at least a category of cases in which the isolated ontogenetic development of a subordinate pattern (or "sub-instinct") contributes to its biological efficiency at a later age, after this pattern has been integrated into a larger whole. There is, however, a category of cases in which such a teleological explanation of the function and ontogeny of hierarchical systems decidedly cannot apply. In the last category most intra-specific or "social" releasers (as defined by TINBERGEN) have to be included, for with regard to them, it would be difficult to imagine any biological improvement in consequence of play exercise. (Unless in species with some kind of "culture" or "civilisation".) With regard to this category, therefore, the question why behaviour is organised hierarchically and why it develops by ascending stages must remain unsolved for the present. We will return to this point in § 3 and § 4 of this Chapter.

But even in the first category, although there is, or might be, evidence of improvement in motor abilities due to "play", the teleological explanation offered by GROOS is not yet exhaustive. The question arises: Why has Nature taken such a complicated way? Why has Nature, so to speak, endowed the young animal with a set of *innate drives* to learn the skills it needs, instead of endowing it with a corresponding set of *innate skills*? In the last case no isolated development nor play exercise of partial patterns would be required and consequently there would be no necessity to waste time in playing and learning instead of spending all available energy on eating much and growing fast. We now arrive at the fundamentals of evolutionary theory. The simple fact that the young animal appears to be able to learn very quickly all the skills it biologically needs for survival might be considered a proof that these skills are in a certain sense *innate* indeed, but can be *aroused* (or *primed*) only by means of *external* stimuli. If so, why are these arousing or priming stimuli localised *outside* instead of *inside* the organism? One cannot assume that Nature has preferred to apply the peculiar technique sometimes used by the obstetrician who, in certain cases, has to make the newly born baby cry in order that its respiratory mechanism will begin to work.

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[1] The process of flash-learning was described as early as 1896 by LLOYD MORGAN when stating that the acquisition of pecking skill in newly hatched chickens "is performed so soon, and with so few trials – often at the third or fourth attempt – that one must regard the whole as essentially congenital in its definiteness, and look upon the few preparatory efforts as merely the steadying of the inherited organic apparatus to its work" (loc. cit., p. 37).

Upon these and similar questions no definite answers can yet be given but some suggestions may be made. Looking at the animal kingdom, there appears to be evidence according to which exercise of biological functions in play during youth occurs especially in those functions which apply to *complicated, incalculable and changing environmental circumstances after adult life is attained* (KORTLANDT 1943). For example, young predatory mammals and birds perform abundant hunting "games", seemingly because their future method of feeding is very varied and requires a high degree of adaptability, whereas grazing and gathering species perform little or no food-seeking "games", seemingly because the relative uniformity in their future food-seeking behaviour makes any learning or training superfluous. Gulls and skuas (*Larus* and *Stercorarius* spec.) when about the age of fledging, perform several types of false hunting and fishing, corresponding to the variety of their natural feeding techniques and food. Terns (*Sterna* spec.) on the other hand, perform little or no food-seeking "games" at all, apparently because one single innate and stereotyped pattern is sufficient to them (AHLQVIST 1937, pp. 167–168). Tree-climbing species seem to perform more climbing "games" than rock-climbing species and these seem to perform more play locomotory activities than species which live on a flat surface. More examples could be added (BUYTENDIJK 1932, 1948). The same principle applies to the perceptual aspect of the problem. For example, in man, chimpanzees and cormorants, i. e. species which are characterised by excellent capacities of sight, the perception of three-dimensional space is largely acquired as a result of learning and flash-learning processes (VON SENDEN 1932, RIESEN 1947, KORTLANDT unpublished). In rats on the other hand, i. e. a species which depends largely on smell, touch and hearing, the visual perception of space is largely innate (LASHLEY and RUSSELL 1934).

So there seems to be a biological relation between the occurrence of *juvenile* play, on the one hand, and the required degree of variability, adaptability and complexity in *adult* behaviour, on the other hand. One might say, metaphorically, that the simpler types of machinery are innate, whereas the more complicated types of machinery become acquired as a result of experience in play. Neurophysiologists may try to find out why this is so, but we may take this tentative conclusion as a working hypothesis for further considerations.

It appears, then, that this provisional suggestion finds support in three sources of factual evidence:

1. According to many findings by LORENZ, TINBERGEN, and other authors, innate releasing stimuli are as a rule very simple and crude, whereas conditioned or learned stimuli are always very complex and detailed. Apparently, learning is apt to accomplish more complicated neural patterns as compared to endogenous maturation.

2. As a rule, a high degree of what might be called "general zoological curiosity" is found especially in those animal species which are preyed upon by a large variety of predators, whereas this type of curiosity (or investigatory behaviour) is relatively little developed in those species which have a relatively small number of natural enemies (KORTLANDT 1943). For example, in the old Dutch decoy industry, wild ducks are trapped by making use of a strangely behaving dog which arouses their curiosity, whereas cormorants or gulls cannot be lured in this way. Further, wild ducks show enormous interest when seeing, for the first time in their lives, a night-heron (a species which is extremely rare in Holland, whereas blue herons are abundant) but cormorants remain quite uninterested on such occasions. In this connection, curiosity might be considered a sensory game with potential predators, i. e. behaviour originating from a sub-instinct participating in the hierarchy of escape behaviour. (Of course, there are different types of curiosity in different species. In predators a fair amount of investigatory behaviour is hierarchically subordinate to food-seeking.)

3. In a relatively large number of cases in which sensory or motor patterns are acquired during infancy, their acquisition is restricted to a definite and limited life-period, and in some of these cases it is even possible to indicate a reason for which such a time restriction is biologically necessary. If such a *sensitive period* is missed, the animal will remain "neurotic" for the rest of its life. Some striking examples of this principle are found in the development of wildness and tameness.

Ontogeny of wildness and tameness

Young cormorants, for example, begin to discriminate between "friends" and "strangers" when about 2 or 2 ½ weeks old. Thereafter, they nevertheless remain relatively tame. They will become very shy, however, and will perform innumerable "vacuum-panics" or "play-panics" when attaining the age of about 9 or 10 weeks, or 2 or 3 weeks after fledging, i. e. at the age when they begin regularly to visit the fishing grounds and other places outside the breeding colony. Before this age there is no special biological reason for being shy, because the colonies are usually on inaccessible cliffs or uninhabited islands, and, moreover, the young bird is then too preoccupied in steadily training its flying abilities and special flying stunts such as the "vertical side-slip" which are preliminary requirements in effective fleeing behaviour. During the period of frequent play-panics and as a result of curiosity, social induction and perhaps other learning mechanisms, the young cormorant gradually learns to discriminate between dangerous and non-dangerous potential dangers, and consequently in protected surroundings it becomes increasingly tame. This development is largely completed when, at an age of 12 to 14 weeks, the young bird leaves the colony on autumn migration, i. e. at the age when proficiency is biologically required. During subsequent years, further taming proceeds extremely slowly, until, at an age of perhaps seven years or even more, under constant environmental circumstances no further marked progress in tameness can be observed.

The very advanced age at which shyness and tameness become shaped in the young cormorant creates a striking contrast to the well known imprinting process discovered by HEINROTH (1910) in goslings: in this species the first and most decisive occurrence with regard to shyness and tameness takes place in the first few minutes of life. Similarly, newly hatched ducklings can be infected by fear of man as a result of one series of loud warning quacks uttered by the mother duck (McDOUGALL 1932, pp. 196–197). The biological reason for the difference with cormorants will be clear, for goslings and ducklings are nidifugous species and are not hatched on an isolated island or cliff.

Similar contrasts are found in mammals. In many, or perhaps most species of this group, tameness and adult sociability are for a large part literally imbibed with the mother's milk, and shyness is largely brought about by the mother's warning cries. The age at which these processes occur shows great differences when comparing nidifugous and nidiculous species. This fact has already been recognised by LLOYD MORGAN (1896).

In hoofed animals (especially the smaller species such as gazelles, sheep, many *Cervidae*) the first day or two of life are often decisive for life. For example, if a lamb is reared by bottle for a few days immediately after birth it will show no sociability towards other sheep when attaining adult life. Scottish sheep farmers know that such lambs cannot be marketed because they cannot be herded when grown up. Scattered and casual observations provide some evidence suggesting that roe and deer calves become shy to man for life if, during the first few days of life, they see or smell man when hearing the mother's warning cry. (See a. o. ALTMANN 1952, BENINDE 1937, HEDIGER 1938, HUDSON 1892, A. MURIE 1944, O. J. MURIE 1951, SCOTT 1945, STEINBACHER 1939, TEGNER 1951.) More critical investigations are, however, still desirable on this point. Similar, but seemingly more complicated processes can be found in domestic cows, according to verbal communications from farmers. In young lambs, fear of dogs becomes established by the ewe's warning bleating (LLOYD MORGAN 1896, p. 119).

Evidently we are dealing here with object-choosing processes as they have been called by FREUD, or imprinting processes as they have been called by ethologists. According to some scanty factual evidence (including verbal communications by zoo keepers) the impression seems justified that an additional shaping of tameness and shyness in hoofed mammals proceeds during the age-period in which many vacuum-panics and similar "fleeing games" are regularly observed. If correct, this would provide a striking analogy to what has been found in the young cormorant, except that in the latter species the first stage of the whole process takes place no earlier than when one-third grown and the second (more influential) stage takes place no earlier than some time after being fully grown.

A very important fact in this connection is that many hoofed animals (especially in the smaller and shyer species) never get rid of their vacuum-panics if they are raised by man in an environment in which no objects for fear occur (ANTONIUS, quoted by LORENZ 1937a, p. 328; LORENZ, quoted by SUTTON 1943, p. 13). In such an environment no object choosing or imprinting of the fear instinct and its sub-instincts (such as fear-curiosity) is possible and consequently a general, vague and objectless "nervousness" develops. Gazelles reared in this way are very susceptible to fatal accidents due to vacuum-panics at a later age. Here we find the curious paradox that an animal becomes timid because it is never frightened. The implications of this fact with regard to human education will be evident.

In apes and man, fundamentally the same development processes concerning tameness and wildness occur but, in comparison with hoofed mammals, development proceeds on the whole at a much later age. This finding agrees with our assumption according to which the biological conditioning period (or periods) of tameness and wildness depends on the biological period (or periods) in which the young animal increases its independence from its mother and becomes confronted with an increasing number of environmental dangers. In this respect apes are especially interesting because, although morphologically they have many of the characteristics of nidifuges, behaviourally they can be considered nidiculous, in so far as they are carried by their mothers for a very long time. From this point of view it is a significant fact that tameness and shyness in apes and man are largely shaped at a much later age than in Ungulates, although according to some psychoanalytical investigations, the influences during the suckling period should not be underestimated. Further, the impression seems justified that object choosing (or imprinting) of shyness proceeds especially in relation to those periods in which the ape or human child demonstrates an increasing tendency to become more independent of its mother in its way of living. In other words, here also the sensitive periods seem to be biologically determined by the necessities of actual life.

It would take too long in this paper fully to review tameness and shyness in ape and man. As an example, the fear of snakes may be discussed here. It is a well known fact that apes, until about six months old, are indifferent to snakes but at a later age become extremely afraid of them. In previous literature there has been much discussion on the question whether this fear is innate or conditioned (e. g. ANTONIUS 1939, HASLERUD 1938, YERKES 1948). Recently, following the great experiment of HAYES (1952) in which a chimpanzee was raised in a human environment from birth, it has become clear that both factors play a role. At the age of about 4 months one day Viki (as the chimpanzee was called), when catching sight of a dangling and snaking electric cord, was suddenly seized with the utmost fear of this cord, although before that time the ape was quite familiar with electric cords (loc. cit., pp. 24–25). It is a significant fact that this occurrence happened at exactly the age at which Viki began to walk and climb freely around, without constantly clinging to her foster-mother. Moreover, after this occurrence Viki appeared to have become very frightened of all dangling electric cords, but *not* of real snakes. Two shattering experiences (at the age of about two years) were needed in order to make Viki afraid of real snakes (loc. cit., pp. 109–110). Therefore we have to postulate in the chimpanzee, at least two mechanisms: 1. an innate general fear of all snake-like objects, which fear matures at the age at which the child's living environment is extended beyond the mother's reach. 2. An imprinting mechanism by means of which this general fear becomes very quickly conditioned to a very restricted class of snake-like objects[1].

Parenthetically, this conclusion is very revealing with regard to a much-contested point in psychoanalytical theory. According to FREUD the fear of snakes, mice, etc., in man is a converted castration anxiety and this castration anxiety is based upon an innate "primal phantasy", which in its turn is supposed to have been evolved during phylogeny as a result of actual castration in primeval peoples. Now from HAYES' observations it seems more plausible to presume, conversely, that castration anxiety and fear of mice in man must be considered a converted fear of snakes in a society where snakes are lacking, and that this fear of snakes is based upon a primeval imprinting mechanism, or primal phantasy directed towards snakes, and that this mechanism, or phantasy has, in its turn, been evolved as a result of actual snake-bites in human ancestors. At first glance this hypothesis may perhaps seem nearly as fantastic as that of FREUD but it provides a biologically more acceptable frame of reference for the facts that led FREUD to his theory. (It may be added that there are some accounts according to which deer behave very aggressively toward snakes and try to kill them with their hoofs. See HUDSON, ed. 1923, p. 159.)

In the scope of this paper, a consideration on the development of "tameness" and "wildness" in man would digress too much. Suffice it to say that a normal child in certain developmental periods will show a well-marked and biologically sound desire for material arousing horror. This desire should be adequately satisfied in an atmosphere of reality in order to secure healthy development and to prevent the establishment of an objectless "nervousness" as described above in Ungulates, but of course it should not be stimulated or primed by means of American horror comics and such like!

In order to avoid confusion it must be added that in this context we are dealing with fright and fear, and not with anxiety (German: Angst). According to psychoanalytical theory, neurotic anxiety (either conscious, e.g. phobia, or unconscious, e. g. conversion diarrhoea) in its strict sense springs from the repression and conversion of drives that threaten other vital tendencies in the personality. In a certain sense, neurotic anxiety might even be considered a synonym of converted unconsumed libido. This means that the concept of anxiety in psychoanalysis is closely related to the concept of displacement-activities in animal psychology[2]. There are, however, continuous transitional stages merging from "anxiety" to "fear" and "fright". For example, the objectless fear in hoofed animals discussed above might equally well be called anxiety in a wide sense. Perhaps future investigations on objectless fears in animals may clarify the problem of anxiety as a whole. On this point the student of animal behaviour is able to make an essential contribution to alleviate one of the most serious scourges of mankind.

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[1] One might also say that the imprinting mechanism for snakes matures at a definite age and then, after being activated by an external stimulus, primes an innate fear directed towards the imprinted object. With regard to Viki no definite choice between both these explanations can be made. The observations of objectless fear or "nervousness" in Ungulates support the explanation given in the main text but there exist also cases (especially in dogs) in which the explanation given in this note seems more justified.

[2] In other words, neurotic anxiety (in psychoanalytical language) might be put more or less equal to allochthonous fleeing behaviour (in zoological language). It would follow that, in man, any repressed impulse is able to spark over to the instinct of fear. This inference, however, seems difficult to reconcile with our present knowledge of displacement phenomena in animals. Therefore the problem of anxiety is still too enigmatic to be dealt with here. It may be added that, at the present time, several prominent psychoanalysts reject the classical anxiety theory rendered above.

It might be conceivable, by way of suggestion, that any newly developing tendency directed towards life-expansion is biologically matched and controlled by a newly emerging susceptibility to imprinting and priming of the instinct of fear. If this suggestion holds good, it might perhaps contribute towards solving the present inconsistency between the psychoanalytical anxiety theory and the zoological displacement theory mentioned above. Moreover, this suggestion might explain a feature which is very conspicuous in most forms of true play but which seems to have been neglected in all existing theories on play: Really playful forms of play are always alternated, accompanied and even characterised by an element of fright and fear, i. e. by cries of distress, expressions of alarm and the like in both animals and man, and by emotions of fright in man. Play is thrilling indeed, or it is no real play. This may explain, too, why the extensive enumeration of games in animals as given by GROOS leaves in most readers the unsatisfactory feeling that most of these games are no true play at all, without being able, however, exactly to indicate what is wrong with them.

This digression on the ontogeny of tameness and shyness will suffice to illustrate the general developmental principle involved in functionless (or playful) arousal, priming, conditioning and learning of instincts, followed by ascending integration. Sources of similar material concerning the development of instincts other than fear are found in BRÜCKNER (1935), HEBB (1949), MEYER-HOLZAPFEL (1949), STEVENS et al. (1951), THORPE (1951), and LEHRMAN (1953).

Biological superiority of acquired patterns

All the material and considerations given in the foregoing part of this Chapter seem to justify the presupposition (implicitly but not explicitly contained in the theory of GROOS) according to which those forms of behaviour that are ontogenetically shaped in isolation from their future vital function, as a result of conditioning and learning, are, after being integrated into the vital system to which they belong, *biologically superior* to those forms of behaviour that are ontogenetically shaped as a result of innate maturation processes. Speaking metaphorically, one might say that (at least in animals) pure science is in the long run superior to applied science and that creativeness is superior to tradition! (See also HARLOW et al. 1950.) The biological superiority of behaviour which is acquired independently of vital needs appears to consist of a higher degree of complexity, variability and adaptability in adult behaviour, in consequence of which the adult animal is able to cope with complex and changing environmental circumstances. Moreover, we must assume that this conclusion applies not only to the motor aspect of behaviour (as suggested by GROOS) but also to the sensory aspect.

This is an interesting result indeed, for at present it seems difficult to see any grounds for considering that acquired behaviour should be generally superior to innate behaviour. We must simply take the fact for granted[1]. When doing so, it follows that the principle of isolated development of partial functions followed by ascending integration at a later age offers great biological advantages to the species, and from this it further follows that a hierarchical organisation of instincts making possible this type of development offers a definite survival value. In other words, hierarchy of instincts *serves to shape non-instinctive behaviour patterns during ontogenetical development.*

§ 2. THE REGENERATIVE FUNCTION OF HIERARCHY

Ontogeny never completed

Having arrived at this point, two objections may be made: (1) The occurrence of what we usually call "play" is not restricted to young or immature animals. Adult animals may be seen playing as well, although less frequently than younger ones. This argument has been raised in the past by several critics of Groos. (2) If hierarchy serves to make feasible isolated development of partial patterns followed by ascending integration, it remains unexplained why hierarchy continues to exist in adult life. For example, one might agree that carnivorous or fishing species avail themselves of a special hunting instinct in order to train them on sham-objects during infancy, but why should an *adult* individual continue to exercise its hunting techniques if it has found other and easier means of subsistence?

Both objections converge in the same direction and both can be answered by the same reply: In matters of behaviour, ontogeny is never completed. In certain ecological circumstances an individual of a predatory species may find its subsistence year after year by exercising only one of its hunting techniques, or even by eating carrion, but nevertheless at any moment this individual must be able to change its way of feeding in case of emergency, and therefore, throughout its life it must continue to train and exercise all the hunting techniques it can call on. A duck may live for years and never meet a predator, but if one day a decoy-dog or a night-heron appears the duck must try to find out what it is, in order to escape potential dangers. The fact that in the case of the decoy-dog, the duck has little chance to survive its curiosity does not alter the general biological value of curiosity, even in very old and "wise" individuals. Other instances will easily come to mind. This means that the continuation of hierarchy after the attainment of maturity may act as a continuation of youth after the attainment of maturity. In other words, hierarchy exerts not only a *formative* but also a *regenerative* function. This is the second main function of a hierarchical organisation of instincts.

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[1] Of course there exist a number of cases in which an incidental explanation of this biological superiority might be offered. Such explanations, however, do not cover the bulk of facts.

From this conclusion we arrive at a second extension of the bearing of GROOS' principle, in addition to the first extension according to which the principle applies not only to the motor but also to the sensory aspect of behaviour. Moreover, by this conclusion we arrive at a very important point in human developmental psychology and psychiatry, which point has been stressed especially by MAEDER (1925), VON MONAKOW (1928), and RÜMKE (1933). This point refers to the positive value of instinctual regression in certain developmental processes and in cases of nervous and mental disease.

When viewing the whole field, two main aspects can be observed with regard to the regenerative function of hierarchy.

First aspect: Prevention of atrophy and monotony

A hierarchy of tendencies correlated to the whole system of activities available to an animal, will prevent or restrict atrophy and extinction of those functions which remain unused for a long time. Such a hierarchy will also prevent or restrict the monotonous repetition and petrifaction of those functions which are used repeatedly and in a stereotyped way. To be sure, BEACH (1945, p. 536) has jokingly rejected the idea that adult lions need hunting games in order to keep their hunting responses in good working order but such a statement can be made only from a laboratory point of view by neglecting the enormous variety of actual circumstances in nature. In human life everybody knows that regular and, more especially, *varied* exercise of one's locomotory abilities is necessary in order to keep them fit. Car-owners know that this principle applies even to cars, at least in some respects! Birds of which the quill-feathers have been regularly clipped for a number of years will gradually lose their flying abilities (SCOTT, quoted by THORPE 1951, p. 21). From this point of view it seems plausible to expect that any behaviour pattern which under certain environmental circumstances might be endangered either by atrophy or monotony will be safeguarded by means of a special instinct or appetite serving to keep this behaviour pattern fit. Moreover, it seems plausible to expect that this principle will hold good not only for motor mechanisms but also for sensory mechanisms. In other words the *mere existence* of a biologically valuable behavioural mechanism will in itself provide an *evolutionary force tending to develop a special instinct or appetite* serving to activate and keep fit this mechanism during the vicissitudes of the individual's life. So that from this point of view, instinctive drives will, in the course of evolution, become as innumerable as there are forms and levels of behaviour, including motor as well as sensory patterns.

There is a fair amount of factual evidence giving support to a widening of the idea of hierarchy as implied in the above suggestion. In zoo-animals there appears to be a lasting tendency to keep in working order all biological functions and behavioural mechanisms that have become useless due to circumstances of captivity although, it must be said, the degree of endogenous stimulation differs from one mechanism to another. All birds of which the wings have been pinioned in infancy will continue to make flying attempts until they die of old age[1]. It seems difficult indeed to find any behavioural mechanism that will become completely idle if it has become useless, except in cases of physical impossibility to exert that mechanism. Further, although captive animals in monotonous environmental circumstances are very liable to habit formation, this state of affairs will never lead to an entirely stereotyped behaviour. On the contrary, there appears to be a lasting tendency to break through even the most stereotyped ways and to use any pattern that has been inactive for a longer or shorter time. In this context the experiments on spontaneous alternation in maze running rats may be mentioned. (See e. g. DENNIS 1939.)

Perceptual sub-instincts

Moreover, this principle seems to apply also to *sensory* mechanisms, in cases in which one and the same motor response can be released by more than one releasing mechanism, or by more than one stimulus situation. It is an old saying that, in hunger and in love, familiarity breeds contempt. The same principle has been found to be valuable in collecting sperm of domestic cattle used for artificial insemination. An important point in this connection is that with regard to the accompanying environmental circumstances during artificial ejaculation, a fair degree of constancy is desirable. The persons handling the bulls, the time of day and similar conditioning factors should be kept as constant as possible. With regard to the place for mounting some little variations have appeared to be favourable. With regard to the dummy used for mounting (either a nymphomaniac cow, a bull, a horse, or a model) however, regular variations have appeared to be essential in order to maintain the bull's sexual urge and, consequently, sperm quality. These experiences have been obtained in different breeds in Holland, England and America. (Verbal communications from specialists in this field; see further ARIENS et al. 1954, p. 26, PERRY et al. 1950, p. 102, ROWSON 1946, pp. 76 79, SMITH 1950, pp. 29-30.) Seemingly, therefore, the principle stated in the proverb holds good only for *innate* and *not* (or in a lesser degree) for *conditioned* stimuli. In other words, there are indications suggesting that, under constant external circumstances, there may occur *internal* (intra-neural) *changes in responsiveness to the composing partial stimuli* that participate in one single innate sign-stimulus, and these changes apparently proceed quite apart from intra-neural changes in responsiveness to the sign-stimulus as a whole. Apparently these changes in responsiveness to the partial stimuli cause the "optimal" sign stimulus to be a variable datum.

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[1] HEDIGER (1942, p. 53; 1950, p. 49) states that there are a few exceptions of this rule, namely in cormorants, but this statement is erroneous, at least with regard to cormorants.

This tentative conclusion fits in very well with some recent investigations according to which there occur in the innate releasing mechanism intra-neural changes in responsiveness to the sign-stimulus in general, quite apart from intra-neural changes in responsiveness which are due to nervous exhaustion or stimulus production inside the *motor* mechanism (PRECHTL 1952, 1953; GLANZER 1953; HINDE 1954). Further, it fits in with the fact that even the mere perception of a reward will act as a reinforcing agency in learning experiments. (References in HINDE 1954.) Finally, it fits in with a new theory on aesthetics launched by VAN WIMERSMA GREIDANUS (1951) according to which aesthetic experience must be regarded as the sensory counterpart of what in the motor sphere is usually called play. At the moment, we are, so to speak, waiting for the discovery of "vacuum-perceptions" ("Leerlaufperzeptionen"), analogous to, but distinct from, vacuum-activities and to be explained by *IRM-specific* (or sub-IRM-specific) endogenous stimulus production. It would be interesting to correlate these phenomena to the distinction made in psychiatry between different types of hallucinations.

From all this evidence a hypothesis may well emerge: Innate releasing mechanisms are not reflex-like blocks (as postulated by TINBERGEN and LORENZ) but true *sub-instincts*, *hierarchically subordinate to the motor mechanisms* or Erbkoordinationen they serve and showing all the characteristics of true instincts (or appetites) such as nervous exhaustion and reloading. (See also HINDE 1954.) Further, an innate releasing mechanism may *in itself* be a minor hierarchical system composed of releasing sub-mechanisms, each characterised by its own rate of nervous exhaustion and reloading, as made plausible by intra-neural spontaneous changes of the "optimal" sign-stimulus. This means at the same time that the term bottom-level instincts (or bottom-level appetites) which was used in Chapters II and III is not quite adequate: the Erbkoordinationen can be considered to be a bottom level only as far as the animal's motor needs are concerned but below this "bottom" there may be a further hierarchical ramification of perceptual needs, each urging towards satisfaction on its own account. (It will be remembered that in Chap. II, p. 191, some evidence was also found indicating that, strictly speaking, the Erbkoordination or fixed pattern can no more be considered the bottom level even in the motor area of behaviour, for during the very first stages of its ontogenetic development it appears to be neither fixed nor coordinated; on the contrary, it develops by fragments that become integrated afterwards.)

In our hypothesis we might go still further and state: the hierarchy of perceptual appetites which seems to operate below the bottom-level of motor and higher appetites, exerts not only a regenerative function but also a pathfinding and priming function with regard to its superordinate levels[1]. Before considering this new point of view (§§ 3 and 4), however, we have first to finish our digression on the regenerative function of hierarchy in general, of which up to now only one aspect (point 1 at p. 231) has been discussed. The question was: Why does hierarchy continue to exist in a latent form after the completion of ascending integration?

Second aspect: Regenerative regression

A second answer to this question can be concisely formulated as follows: *Hierarchy serves to make possible regenerative regression.* In order to make this point clear, a short introduction will be necessary and some concepts have to be defined.

As explained in Chap. I, according to Freud, subordinate instincts mature, become conditioned and find their goals more or less independently of each other and often at different ages. At a later age, when these partial instincts become integrated into larger units, and at a still later age when these units in their turn become integrated into still larger wholes, it may naturally occur that the building stones appear not to fit in with each other. Consequently, in order to accomplish integration in spite of this, a re-modelling or reshuffling of the building stones will be necessary. In other words, the objects and goals toward which the partial instincts during ontogeny have become conditioned, have to be re-developed. This process often requires a reconditioning of the partial instincts and this reconditioning proceeds by means of a revival of infantile forms of behaviour. In such cases the individual will try to find satisfaction by means of objects or activities which have been obsolete for many years and as a result in many cases a reorganisation of low-level behaviour will follow. Such a return to infantile patterns of behaviour is called *regression.* Two types may be distinguished: regression to an infantile object and regression to an infantile level of instinct organisation, but as a rule both types occur together. During psychoanalytical treatment, regression is deliberately evoked and used as a therapeutic technique.

For the sake of completeness it must be added that the characterisation and paraphrasing of regression as given here is a rather simplified and incomplete one, condensed to come within the scope of this paper. Furthermore, we are especially dealing here with the *regenerative* function of regression ("integrative disintegration" RÜMKE) and therefore the more pathological forms of regression ("dissolution" JACKSON) are left out of account. It was especially the Zürcher school which drew attention to the positive merits of regression (a. o. MAEDER 1925, 1928, also RÜMKE 1933) whereas FREUD predominantly emphasised the more negative or pathological aspects[1].

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[1] The same statement applies to those sensory appetites that can be localised at a higher hierarchical level than the minor ones under discussion here, as has been demonstrated above with regard to curiosity.

From the foregoing it will be clear that regression can be possible only if a hierarchical organisation of instincts continues to exist latently after the completion of ascending integration, as otherwise the steps required for descent would be missing. We now have to ask whether regenerative regression in animals does occur.

Scarcity of evidence on regenerative regression

A survey of existing literature yields extremely meagre results. It is true, in American literature dealing with experimental neurosis, much material can be found with regard to regression, but next to nothing of this material refers to the positive and healthy type of regression we are searching for. (See e. g. GANTT 1944, MAIER 1949, MASSERMAN 1946, MOWRER 1940.) In European literature dealing with imprinting one finds many cases of pathological fixation to an object as well as to an organisational level, and moreover some cases of recovery from a pathological fixation have been reported (THORPE 1951, p. 263), but in none of these cases is there clear evidence suggesting that this fixation has been healed by the intermediacy of a regenerative regression. In this respect contemporary animal psychopathology is quite similar to early Freudian psychoanalysis: human beings are often more curious about mental disease than about mental health!

A biologically valuable type of alleged "regression" in insects was mentioned by BRUN (1926, pp. 24–25) but in this case the observed type of regression cannot be considered a "réculer pour mieux sauter", and further, the term "regression" was used in rather an aberrant meaning. Not long ago, in a very interesting paper on the ontogeny of instincts, MEYER-HOLZAPFEL (1949) reviewed a number of cases in which seemingly infantile activities were performed by adult animals and all these cases were classified as cases of "regression". With regard to her opinion according to which courtship-begging in female birds should be considered regression, however, some doubt may be justified: as long as we cannot find out why courtship-begging is restricted mainly to females, no final interpretation is possible. For the rest, in her account two cases were mentioned (quoted from LEVY and from KATZ) which do suggest the regenerative type of regression. In both these cases, regression appeared to occur when the animal was transferred to a new environment.

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[1] Recently, in animal psychology, the term "regression" has been used to indicate the atrophy of an instinct (THORPE 1951, p. 21). This usage of words is highly confusing and should therefore be abandoned.

It may be added that phenomena related to regression (as defined above) are found not only in behaviour but also in physiology. During the ontogeny of man, erythrocytes are produced first in the spleen, thereafter in the liver and finally in the bone marrow. In cases of disease the reversed sequence may be observed: at first the liver and thereafter the spleen may resume the production of erythrocytes. It is quite possible that behavioural regressions may often be based upon hormonal factors but little or nothing is known of this.

A case of regression observed in cats and described by WESTERMAN HOLSTIJN (1950, p. 100) may be quoted here (translated): "A young cat was already independent and house-trained for quite a time. When her brother to whom she was much attached was given away to another home, she joined up with a mother cat who had kittens, which at that time happened to be in the house, crept into their basket and commenced to suckle again, and, moreover, started to urinate in the basket." In this case of observation the regression itself and its cause are very clear but its ultimate effect with regard to a subsequent reorganisation of behaviour remains obscure.

As a result of several investigations it has been proved that, at least in mammals, deprivation of an instinct or sub-instinct during infancy and youth may often cause a strengthening of the tendency in that instinct and a failure of ascending integration at a later age or at the attainment of maturity. KUO (1931) has found that kittens when raised in isolation show a marked tendency to respond to rats by playing and false-hunting with them. According to HUNT (1941) infant feeding-frustration in the rat when followed by adult feeding-frustration causes 2 ½ times as much an amount of hoarding behaviour as compared to the amount of hoarding observed as a result of adult frustration without previous infant frustration. Dogs and rats, if restricted in their exploratory possibilities early in life, show at later ages significantly more exploratory behaviour than normal dogs and rats do (THOMPSON and HERON 1954). Monkeys will become persistent thumb-suckers if fed by means of a medicine dropper during the first 6 weeks of life (HARLOW 1951). In a chimpanzee, restricted opportunity for tactual, kinesthetic and manipulative experience during the first 31 months of life appeared to lead to a loss of sensitiveness to pain and discomfort, supplemented by an excessive need for pleasure derived from tactual-pressure stimulation (NISSEN, CHOW and SEMMES 1951). More instances of the same principle could be added. (See especially MASSERMAN 1944, pp. 151–155, and MASLOW 1948.) From these and similar observations it seems that these animals in this way try to make up for the play period which they have missed earlier in their lives. One is even reminded of NIETZSCHE's lament: "Ich überspringe oft die Stufen, wenn ich steige, – das verzeiht mir keine Stufe." (Zarathustra I, Vom Baum am Berge.) Translated: "Often I jump the steps, when ascending, – but this does not let me off any step." In any case, however, these papers deal with fixation and not with regression. Consequently no valid proof of our suggestion is found in them.

Regenerative regression in the cormorant

It appears that, except for man and the two cases mentioned by MEYER-HOLZAPFEL, the cormorant is the only animal species in which fair evidence pointing to the regenerative type of regression has been observed. This material, however, has not been published until now and therefore a short summary may be given here.

The first three months of life of the young cormorant may be characterised as a growing up towards individuality and independence, ending by the young bird's leaving the colony on summer migration. This development is by no means a straightforward or gradual one; on the contrary, it proceeds in 5 developmental jumps (in some individual cases, in 6 jumps) each of them taking no more than a few days. Each of these developmental jumps is characterised by a reorganisation of the young bird's behavioural organisation and at the same time by a reorganisation of its "Umwelt" organisation, both phenomena being aspects of one and the same process. In the last three of these developmental jumps, progression is preceded by regression. This feature suggests that a regenerative regression will not occur until a certain height and complexity of organisation has been attained. At the lower levels during ascending development, the building stones will naturally fit in more easily than at the higher ones.

Until about 2 to 2 ½ weeks old the young cormorant is still unable to put its locomotory abilities to the service of its vital needs. It is the legs which move the chick and not the chick which moves the legs. Or, in other words, the young bird *is moved* by creeping instead of *moving* by creeping. Consequently in the chick's "world", or "cosmos" (Umwelt) there is, at this age, still no difference between "far" and "near". Its behaviour often reminds one of that of a human baby who is trying to get hold of the moon. Physical space is not yet perceived as "space" in the psychological meaning of the term.

At the age of 2 to 2 ½ weeks, creeping movement becomes integrated into alimentary, investigative, defensive and other vital behaviour. Consequently the nest area acquires the characteristics of true three-dimensional space. This radical reorganisation may be called the first step towards individuality and independence. In it the developmental process takes a straightforward and unequivocal course, which is not surprising, for we are still dealing with the bottom of the integrational system. After this reorganisation the chick's outer world outside the nest area still remains a two-dimensional "end plane" ("Fernste Ebene", VON UEXKÜLL).

The second developmental jump is fledging which takes place as a rule at an age of 7 weeks. (Cases of premature fledging are left out of account.) A few days before fledging, the nestling becomes increasingly interested in the scenery around its nest, and at the same time, a rapidly increasing motor restlessness arises. The young bird starts climbing about in the branches, practises gymnastics there with increasing boldness, makes prolonged false flying-movements, or even little jump-flights, walks from the perch to the nest-rim, and back from the nest-rim to the perch, and all these activities are interrupted from time to time by the bird's absorbtion in intently gazing at the scenery. Nearly all interests in vital needs, even in food, are gradually lost. The young bird seems eaten up with "Wanderlust" or "Hinausweh", longing for space. Finally the stress breaks out: the first sortie is made. Thereafter, as a result of flash-learning and imprinting processes, at an amazingly quick rate (usually in 2 days) the fledging will become familiar with spatial relations in the nesting trees. Its Umwelt outside the nest area is reshaped into a true three-dimensional one and it flies to and fro without any trouble or hesitation. In addition to this, all symptoms of restlessness and "Hinausweh" disappear, new habits in line with the parents' habits are formed and life becomes stabilised again. The second great step toward individuality and independence has been accomplished. From this point of view, the preliminary motor restlessness and sensory "Hinausweh" preceding its consummation may be considered appetitive behaviour (CRAIG), or symbolic behaviour (PORTIELJE), or a syndrome of damming up of libido (FREUD), or something like that. In any case, our description has shown that this time the course of development was not unidirectional and unequivocal. On the contrary, in the preliminary phase the young bird, so to speak, groped and reached for its way, trying and exploring everywhere, searching for more space where it could, until finally all these diffuse energies became canalised into the only way still left open to them: fledging. On the other hand, however, in this introductory behaviour no true regressive element can be seen, for all this groping and reaching, trying and exploring, was of a definitely progressive and prospective nature. The second developmental step is of a higher type than the first one but the organisation of behaviour has not yet attained a level at which a *preparatory regression* is required. We will return to this point later on (pp. 241 and 258).

The stabilisation of habits and ways after fledging is not durable. In the course of 1 or 1 ½ weeks (in some cases 2 weeks) following the first sortie, owing to subsequent maturation and acquisition of flying skill, the young bird's spatial life-habits (e. g. habitual flying routes, landing branches, perching places, etc.) gradually become outmoded. Moreover, many of these habits were formed accidentally or were copied from the parents' habits during the first two days or so after fledging. Consequently they do not suit the young bird's needs and a tendency towards individuation (i. e. shaking off copied habits) becomes apparent. At first, new symptoms of restlessness and Hinausweh emerge. In many cases the young bird again begins to explore and rove from branch to branch in the trees around its territory, much in the same way as before fledging. The daily number of hours spent in the tree-group where it hatched shows marked fluctuations and sometimes the young bird will spend a night elsewhere. Most customs and habits are broken, temporarily or for ever, often in a rather futile way, and often showing great individual variation. (E. g. nest-companions that were accustomed to sleep together may one day prefer to sleep apart, and those which were accustomed to sleep apart may one day prefer to sleep together.) In short, in addition to the revived syndrome of Hinausweh, the young bird shows the syndrome of "negation of the until-now" ("Verneinung des Bisherigen", a term applied by Ch. Bühler, 1922, to characterise the first phase of human puberty). A complete regression is shown. This phase is followed by a progressive one, lasting a few days, during which the young bird chooses new habitual alighting, perching and sleeping places and a new territory which is defended against intruders, and so on. All irregularities of life-habits disappear and the daily number of hours of presence in the home neighbourhood becomes fairly constant again. Infantile fixations have now been overcome and *individuation* has been accomplished. Thereby the third great step towards individuality and independence has been achieved, and a new level of pre-independent behavioural organisation has been attained.

About 1 ½ or 2 weeks (in extreme cases, 1 or 3 weeks) later, i. e. 3 or 4 weeks (in some cases 5 weeks) after fledging, a further period of unrest, disturbance, Hinausweh and "negation towards the until-now" sets in. The symptoms are exactly the same as in the foregoing cycle but they are even more conspicuous and their variety is still greater. Moreover there are even more individual differences between one young bird and another. For the rest, however, the symptomatic picture is exactly identical to that described above. Even the exploring and roving from branch to branch is seen again. Subsequently, in most cases the young bird will be absent from the colony for 1 or 2 (sometimes 3) days and nights. On its return the order of customs and habits is broken again and a new one established; but this time (at least in most cases) no new territorial bonds are entered into. Often the young bird remains "territoryless", i. e., even if it shows a preference for one particular nest, this nest will not be defended against intruders any more, nor will the preferred perches be defended. Therefore this cycle may perhaps be adequately characterised as a *breaking of territorial bonds*, at least in the majority of individuals. It is the fourth great step towards individuality and independence. As a result of this phase, nesting behaviour often attains an organisational level identical to that which is found in most one year old birds in spring. (See Fig. 5.) The family-ties with parents and siblings, however, remain intact as a rule.

The fourth developmental step is again followed usually by some days of stable habits. Thereafter, roving and exploring may set in again, habits become irregular, sleeping places may be changed, etc. After these introductory symptoms, the young bird will as a rule be absent from the colony for a few days and thereafter it will return again and enjoy its parent's feeding; but this time, as a rule no new habit-formation occurs. For, within 2 or 3 days the young bird will disappear, not to be seen again until next spring, if then. The fifth developmental step has led it to full independence at an age of 12 to 13 weeks, in extreme cases 11 ½ to 14 weeks, i. e. no less than 4 ½ to 7 weeks after fledging. Childhood is over now. The young bird has left the colony for the coastal sands and flats and it will soon depart from there on its long and risky journey to France, Spain and even Tunisia. In the colony the parents give their call-notes in vain.

Nature of "re-progressive symptoms", or "ruptural behaviour", or "amoebic activities".

When surveying the whole sequence it will be clear that we are dealing with *one single* but step-like proceeding process. Each successive developmental jump can be considered to be a topographical life-expansion of the individual as well as an autonomisation or "self-realisation". In each successive jump a link with and a dependence on the parents is severed (which may be called a step towards individuality), and at the same time in each jump a new relation to, and a new task in the outer world is established (which may be called a step towards independence). Moreover, each successive jump can be considered an anticipatory stage toward the next one. In each of them the young bird, by its symptomatic Hinausweh, its negation toward the until-now and its temporary absences feels and reaches out, so to speak, toward full independence, which goal, however, remains out of reach so long as the intervening stages have not been passed through. It is quite natural, therefore, that at the end of each cycle the urge finds its condensation and crystallisation in making the next necessary step and consequently the urge appears to be satisfied during the ensuing few days. Apparently the urge must swell and be dammed up for several days before it is strong enough to break through the conservative resistance and set in a new rupture of behaviour. Considered in this way, we must assume that the developmental libido (or "instinct formatif" as it was called by von Monakow) exerts a *continuously* proceeding process, which process however results in a *discontinuous* and rhythmical series of effects. The reason for this is quite a simple one, for the number of organisational levels of behaviour is restricted, and consequently the animal must necessarily jump from one level to another[1].

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[1] The reader might object that this process is interrupted by a period of latency, lasting from 1 ½ to 2 weeks after fledging until 3 or 4 weeks after fledging, as mentioned above, which fact contradicts a continuous process. It may be added, therefore, that in this period, developmental libido is used up by the ontogenetic develop-

(see cont. p. 241)

From this point of view, the regressive symptoms in the introductory phase of a cycle are regressive and progressive *at the same time*. One might more aptly call them "*reprogressive*" symptoms, or something like that, in order to distinguish them sharply from the pathological type of regression which is only a relapse. One might also call them "*ruptural*" behaviour in order to indicate that in them no definite "texture" of behaviour can yet be discovered. Or one might even call them "*amoebic*" activities in order to indicate their formlessness and multiformity at the same time. All such terms are only words. The essential feature is that in these vague behavioural phenomena a new instinctive urge which has *no form, no object and no goal yet*, tries to find its shape and expression. It is exactly the *absence of any definite instinctive outlet* for this urge which determines its multiformity and variability. Consequently these behavioural phenomena might be described at the same time as intention movements, as displacement activities, as appetitive behaviour and as non-innate trial-and-error behaviour. They seem to be found at the common root of all these more distinct types of behaviour, in the same way as *Amoeba* is found, so to speak, at the root of all living nature. In this groping and reaching toward the future there is no true distinction between reshuffling and pathfinding, or between breaking and making. Regression and progression are aspects only of one and the same process by means of which a vague urge is trying to canalise its way and find its new shape. (See, however, § 4, p. 258.) Metaphorically speaking, one might say that the young bird is searching through its abilities in order to find the instinct the urge of which is pressing. Here again (as in § 1, p. 231) the demarcation between instinctive and non-instinctive behaviour appears to fade.

Ruptural symptoms of a similar type as described above are well known in the introductory phase of developmental jumps in man, especially in puberty but also in other decisive life-periods. (E. g. symptoms of "Sturm und Drang", symptoms of "life begins with forty", etc.) Similar phenomena occur also during certain phases of psychoanalytical treatment and in the creative periods of artists and scientists of an intuitive type of mind.

In animals some features of ruptural behaviour have been recognised by PORTIELJE (1948) and were described as follows: (translated) "In youth or in renewed initiation this as yet incompletely performed behaviour gradually manifests less or more differentiation and also integration, and finally it is accomplished with the real instinctive object and in the proper natural setting. During this process, species-innate goal-striving is regulated by subjectively experienced pleasure and pain, stimulated by objectively excited emotions and primed by environmental situations (characterised by imagos and acting as symbolic goal-objects) until such a level is

(cont. note p. 240)
ment of other behaviour systems, as expounded briefly in Chap. II. More details will be given in a forthcoming book on "Texture and Tecture in the Behaviour of the European Cormorant".

reached as is necessarily required for a complete realisation of its biological intention." (loc. cit., p. 184.) Or, in plain words: Innate behaviour develops from a rather vague to a clear-cut state, and in this maturational process, the regulating, stimulating and priming influence of external factors is required in order that full integration shall be accomplished. To this, PORTIELJE added a quotation from the philosopher WHITEHEAD: "Symbolic expression of instinctive forces drags them out into the open, differentiates them and delineates them." From all this it will be clear that PORTIELJE recognised the element of groping, reaching and path-finding in this type of behaviour and also that he recognised we are here in a sort of no-man's land between "innate" and "acquired" although for the rest he did not recognise the rhythmical and cyclical sequence of developmental jumps. Unfortunately, however, this type of behavioural symptoms was classified by him together with several other types of activities under the heading of "symbolic activities" and consequently their separate nature (as compared to phylogenetically or ontogenetically stabilised symbolic activities) has remained unnoticed by his readers. In PORTIELJE's terminology this type of activities might have been appropriately designated as "primary symbolic activities" in contrast to the innate and the neurotic types.

Imprinting and regeneration

It is a curious fact that until now no evidence pointing to the occurrence of regenerative regression has been found in other animals than the cormorant, except for the two cases quoted by MEYER-HOLZAPFEL. On theoretical grounds one might expect regenerative regression to be a very common phenomenon indeed in all animal species which are characterised by a fairly complicated behavioural organisation, for the principle of ascending development may easily cause the building stones not to fit in with each other during the later stages of ontogeny. It would be surprising if Nature had failed to make provision for such cases.

In order to clarify this point we may consider some aspects of the phenomenon of object-choosing, as it was called by FREUD, or imprinting (Prägung), as it was called by HEINROTH. We have seen that, in the course of ontogeny, the bottom-level instincts at first mature independently of each other, and that afterwards these instincts become united into the next-to-bottom instincts which in their turn mature independently of each other until, at a still later age, they in their turn become united into still larger units, and so on. Consequently if in the earlier stages of development a particular sub-instinct has become accidentally conditioned to an abnormal type of object, at a later stage its superordinate instinct will also appear to be conditioned to an abnormal type of object; for, as we know, the more complicated object toward which a higher-level instinct is directed, is largely composed of a mixture of characteristics which are derived from the more simple objects toward which its subordinate instincts are directed[1].

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[1] Imprinting has sometimes been called conditioning in the absence of a drive and a reward. Actually, however, the young animal shows appetitive behaviour toward

(see cont. 243)

Now at first glance one might expect that the characteristics of the higher-level object will be a simple adding up of all the characteristics of all the subordinate lower-level objects. Actually, however, this is by no means the case. On the contrary, no man will ever fall in love with a woman who is in all respects (physically and mentally) exactly identical with his mother twenty years previously, although no doubt he will be very interested when meeting such a woman. Similarly, no man-reared jackdaw will ever fall in love with the man who has reared it from its earliest infancy, although no doubt it will fall in love with one or another human being as soon as maturity is attained (LORENZ 1935, p. 172.) Analogous cases of neurotic "object transference" (according to psychoanalytical terminology) in geese have been described by THORPE (1951, p. 172) while their counterpart may be found in HEINROTH (1910, pp. 652–654) where the spontaneous divorce of incestuous pairs of immature geese has been described.

From all this it appears that there must be certain remodelling, transforming, or regenerating forces or agencies which exert their influence in the intermediate period between the conditioning of the lower levels and the maturation and integration of the higher levels. Further, we must assume that in this regenerative process, newly maturing innate components are added to the characteristics of the object and will be amalgamated with them. It is especially STEINBACHER (1939) who has recognised the importance of this last-mentioned point with regard to imprinting processes in animals. According to his account: "When growing older, young animals which have been imprinted to man often appear to join members of their species from the first moment onwards and without any trouble ... Perhaps this may be explained by assuming that certain characteristics of the releasing pattern of the species-companion (Artkumpan) are innate but start to work not before development is well advanced... If, however, young animals that have been reared in isolation continue to have contact exclusively with human beings for a very long time, then as a result these innate recognition characteristics will be covered up again... During ontogeny, the releasing pattern of the species-companion seems to develop from the releasing pattern of the parental companion, but, in

(cont. note p. 242)
the imprinting object, so there must be a drive, and further there is a reward also. The point is that, in the sensitive period, the *bottom-level* instinct is rewarded and that, at a later age, the resulting pattern is adopted by the *higher-level* instincts without any *further* reward. (See also Chap. I, point 4 according to FREUD, and Chap. III, p. 211 and p. 219.) Further, in order to prevent confusion, it must be remembered that we are dealing here not so much with objects by which reactions are elicited, but rather with objects by means of which satisfaction can be gained, or at least abreacting can be accomplished.

this process, innate components which emerge not before a more advanced age has been attained seem to play a role as well." (Translated from loc. cit., pp. 304–305.)

All such processes are included under the concepts of "transformation of libido", or "vicissitudes of instincts" discerned by FREUD. Considering that, after full maturity has been attained, as a rule all subinstincts belonging to one functional cycle become directed towards one and the same object, we may be pretty sure that in animals the regenerative processes are able to cope with very difficult cases indeed, that is to say with cases which in man would require the help of a professional psychoanalyst. It is these regenerative processes which are responsible for what THORPE (1951) has called the "generalisation of the (sensory) pattern" in imprinting (loc. cit., pp. 260–261). Only in the most extreme cases, for example in the turkey described by RÄBER (1948), will a lasting dissolution of the animal's behaviour system follow, which outcome might be called an "experimental neurosis" in optima forma. With regard to such extreme cases THORPE stated: "A number of observations suggest that once imprinting to the 'right' object is prevented the whole behaviour pattern is liable to be disrupted, with the result that one piece gets attached to one imperfect object, another to another, and the various mating and social reactions may become attached to almost any object except the correct one." (loc. cit., p. 261). Such cases, however, are very rare indeed and therefore it is a surprising fact that up to now so little is known of the regenerative processes preventing such cases coming into being.

§ 3. THE PRIMING FUNCTION OF HIERARCHY

Hitherto in this paper, we have regarded hierarchy as essential a system of appetites each of which represents a specific goal, thereby implying that the animal may pursue a lower or middle level goal either in order to attain this goal for its own sake or as a means to attain a goal of higher order. In other words, a superordinate appetite is assumed to be able to use and operate all its subordinate appetites as tools, or as intermediate goals by means of which the superordinate goal will ultimately be accomplished. This implies at the same time that all efferent impulses, when elicited, are assumed to flow off downwards from instinct to instinct (i. e. from centre to centre) until they are discharged in a motor outlet (either half-way or at the bottom), or until, in the end, the superordinate instinct from which they originate is satisfied and consequently ceases to produce nervous impulses. (The third possibility, viz. that the impulse sparks over to a displacement activity, may be left out of consideration for the moment.) According to this picture, hierarchy must be considered as a *one-way* traffic system.

There is, however, some factual evidence suggesting that this picture is an incomplete one. Apparently, in the long run a subordinate instinct, especially when regularly and strongly activated by environmental stimuli, is able to *prime the tendency* of the instinct next above it. This would mean that in a hierarchical system, there is not only a short-term one-way *downward* traffic of *actual impulses* but also a long-term *upward* (or perhaps two-way) traffic of *tendencies*. The word "tendency" should be taken here as a technical term, as defined on p. 189. Or, in other words, momentary impulses can travel only downwards but a prolonged state of frequent external stimulation of a lower or middle level instinct may cause an upward influence resulting in a lasting, or even permanent state of hyperactivity of that next above it. (One might remark that a similar phenomenon is found in *social* hierarchies, e. g. in an army at war; but in this case the state of hyperactivity of the higher levels does not last long after the external "stimulation" of the lower levels has ceased!) A scheme is given in Fig. 10.

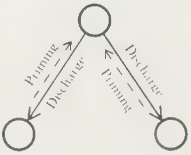

Fig. 10

Evidence of upward priming

Evidence pointing to this type of interaction may be derived from various sources.

First of all, teachers and educationists have recognised that too much fondling as well as much punishment may accelerate and prime sexual development in children. In particular the confessions of Jean Jacques Rousseau have contributed to the spreading, on the European Continent, of the idea that beating on the buttocks is apt to arouse sexual urges and may, in some boys, even cause erection and orgasm. Nowadays this idea also seems to extend to the staffs of some English boarding schools (Chesser 1941).

Secondly, the importance of priming in its relation to a hierarchical organisation of instincts was recognised by Freud as early as 1905. The following quotations from his "Three Essays on the Theory of Sexuality" will illustrate this point and give at the same time a teleological explanation of its biological use: "We may expect that Nature will have made safe provisions so that the experience of satisfaction [of infantile sexual instincts by means of erogenous zones] shall not be left to chance... The contrivance that fulfils this purpose in the case of the labial zone... is the simultaneous connection which links this part of the body with the taking in of food... Like the labial zone, the anal zone is well suited by its position to act as a medium through which sexuality may attach itself to other somatic functions... The intestinal disturbances which are so common in childhood see to it that the zone shall not lack intense excitations... The anatomical situation [of glans penis and clitoris], the secretions in which it is bathed, the washing and rubbing to which it is subjected in the course of a child's toilet, as well as accidental stimulation (such as movements of intestinal worms in the case of girls) make it inevitable that the pleasurable feeling which this part of the body is capable of producing should be noticed by children even during their earliest infancy, and should give rise to a need for its repetition... It seems that the fullest provisions are made for setting in motion the process of sexual excitation – a process the nature of which has, it must be confessed, become highly obscure to us... The decisive element in these sources of sexual excitation is no doubt the *quality* of the stimuli, though the factor of intensity, in the case of pain, is not a matter of complete indifference. But apart from these sources there are present in the organism contrivances which bring it about that in the case of a great number of internal processes sexual excitation arises as a concomitant effect, as soon as the intensity of those processes passes beyond certain quantitative limits... A child's intercourse with anyone responsible for his care affords him an unending source of sexual excitation and satisfaction from his erotogenic zones. This is especially so since the person in charge of him, who, after all, is as a rule his mother, herself regards him with feelings that are derived from her own sexual life: she strokes him, kisses him, rocks him and quite clearly treats him as a substitute for a complete sexual object. A mother would probably be horrified if she were made aware that all her marks of affection were rousing her child's sexual instinct and preparing for its later intensity. She regards what she does as asexual, "pure" love, since, after all, she carefully avoids applying more excitations to the child's genitals than are unavoidable in nursery care. As we know, however, the sexual instinct is not aroused only by direct excitation of the genital zone. What we call affection will unfailingly show its effects one day on the genital zones as well. Moreover, if the mother understood more of the high importance of the part played by instincts in mental life as a whole – in all its ethical and psychic achievements – she would spare herself any self-reproaches even after her enlightenment. She is only fulfilling her task in teaching the child to love. After all, he is meant to grow up into a strong and capable person with vigorous sexual needs and to accomplish during his life all the things that human beings are urged to do by their instincts. It is true that an excess of parental affection does harm by causing precocious sexual maturity and also because, by spoiling the child, it makes him incapable in later life of temporarily doing without love or being content with a smaller amount of it." (loc. cit., Ges. Werke, V, pp. 85–125; Stand. Ed. VII, pp. 184–223).

Thirdly, similar phenomena have been demonstrated in the male three-spined stickleback by van Iersel (1953). According to his account, in this fish a distinction of three hierarchical levels can be made: the top-level is represented by the reproductive "drive", the middle-level by e. g. the parental "drive" and the bottom-level by e. g. the fanning "drive"[1]. He found that "eggs do not only have an immediate releasing effect but help to build up the drive as well", and further, "very probably, the eggs do not only prime the fanning drive, but also the reproductive drive as a whole, which drive must be superordinated above the sex and the parental subdrives." (loc. cit., pp. 98 and 135). In other words, *external* stimulation of a bottom instinct during a longer span of time causes a gradual increase of the *endogenous* stimulus production in the superordinate instinct. A similar phenomenon was found in Cichlid fish by Baerends (verbal communication).

It may be added that the term "priming" in its technical sense (as it has been used in this paper) is derived from van Iersel, although van Iersel still uses it as a colloquial word. This term seems preferable to the psychoanalytical equivalents "excitation" (Erregung) and "arousal" (Wecken), for these have several other connotations. Of course the concept of priming need not necessarily imply an upward process in a hierarchy: there may also be a downward priming and a priming in one single instinct. The last mentioned type has been recognised also by McDOUGALL.

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[1] In his paper the term "drive" seems to have been used in a twofold meaning: (1) as a synonym of our term "tendency" as defined on p. 189, (2) as a synonym of Tinbergen's term "instinct" or "centre". Fanning is a special activity by means of which the eggs in the nest are ventilated.

A fourth source of evidence with regard to upward priming is perhaps found in practical animal husbandry. In domestic cattle some bulls appear to suffer from a subnormal sexual urge, or from an inadequate extrusion of the penis. In some cases this defect can be cured by placing the bull for some weeks in a field, together with a number of cows. This procedure, however, is only successful in fairly young bulls. Apparently, play between bull and cows augments the sexual potency of the young bull. After the bull has been returned to his stall, the improvement in his serving and extrusion capacities appears to be lasting, although not in all cases (verbal communications from specialists in artificial insemination). If the result were caused exclusively by conditioning, one would expect an immediate relapse to be the rule after the bull had been returned to his stall, for bulls are very sensitive to environmental changes. Therefore, apparently, the cure must be attributed to a priming process. More research on this point is desirable.

A fifth source of data may perhaps be found in American literature on conditioning and learning. It seems plausible that many cases of so-called "conditioning" and "learning" are actually cases of priming. This might apply e. g. to the ontogeny of feeding and hoarding behaviour in rats (BIRCH and RIESS, quoted by BEACH 1951, HEBB 1953, and LEHRMAN 1953). In view of the wealth of literature, however, the writer feels incompetent to make any definite statement on these points.[1] Other evidence suggesting the priming of pain and social behaviour in chimpanzees has been given by NISSEN, CHOW and SEMMES (1951).

As a sixth source, some castration experiments may be considered. It is a well-known fact that in many species of mammals, including man, castration when applied after puberty often exerts little effect on sexual motivation and potency, whereas castration before puberty results in a considerable reduction of the sex drive. From this it seems plausible that testicular hormones act both as stimulating and priming agents. Here the difficulty is, however, that the student of behaviour goes out of his own domain because the physiological aspects of this matter cannot be left out of account. For the rest the question, what sort of physiological processes may be underlying priming, has to be considered separately as long as we know so little about the occurrence of priming itself.

Finally, as a seventh group of data relevant to this problem, some neurophysiological experiments by HESS and BRÜGGER (1943) may be mentioned. By means of electric stimulation of the hypothalamus in cats these authors were able to localise a hierarchical system of nervous centres controlling urination and defaecation. By choosing the appropriate area of stimulation either the complete pattern (including appetitive behaviour) or partial patterns could be elicited at will. In the course of these investigations it was found that "there is a marked tendency toward mobilisation of the complete mechanism belonging to the complete performance, even if only a partial performance is directly induced." (translated, loc. cit., p. 531). Now it must be admitted that this result is only a case of upward excitation instead of upward priming in the hierarchical system, but nevertheless it is an important finding in this context because it contributes to a clarification of the whole process.

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[1] In other experiments taken by BIRCH the development of the maternal instinct in female rats was investigated. He raised rats fitted from an early age with "Elizabethan ruffs" preventing oral and nasal contact with the genitalia. According to the published accounts, these rats showed a defective and disrupted maternal and nesting behaviour even if the ruffs were removed during the last stages of pregnancy. A repetition of these experiments by H. E. COOMANS (Zoological Laboratory, University of Amsterdam) suggests, however, that (1) presence or absence of a ruff at an early age is irrelevant, (2) presence or absence of a ruff during parturition is decisive, (3) if the ruff is removed immediately after parturition, or at a later stage of the reproductive cycle, normal maternal behaviour will be restored within two or three days. The experiments are still in progress.

From the foregoing we may conclude that the upward priming function of hierarchy has been definitely proved in man and that it may be accepted at least as a plausible working hypothesis in animals. (See also the conclusions drawn in § § 1 and 2 of this Chapter, pp. 225, 229, 230 and 235.) If this hypothesis is taken for granted for the time being, we are able to explain a curious aspect to be considered now: viz. what might be called the apparent "asymmetry" of hierarchical systems.

Asymmetry of hierarchical systems

In order to elucidate this point we can make a schematic drawing of a hierarchical system. In doing so, we will arrange instincts of the *same level* from left to right in the order in which they successively mature during ontogeny or seasonal maturation. (As discussed earlier, instincts of *different* levels mature in a sequence leading from the bottom to the top.) Now at first sight one would expect the scheme to be a symmetrical and isosceles one as represented in Fig. 11a. Actually, however, in many cases in which the ontogeny of a hierarchical system has been studied, an asymmetrical type is found, as represented in Fig. 11b, or even the type indicated in Fig. 11c, or at least an intermediate type between a, b, and c. (The symbols are the same as used in Figs. 3–6.)

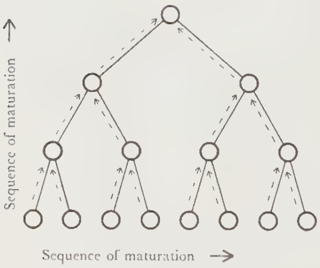

Fig. 11a

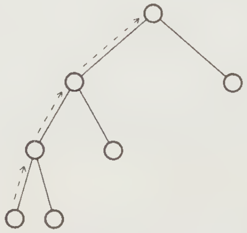

Fig. 11b

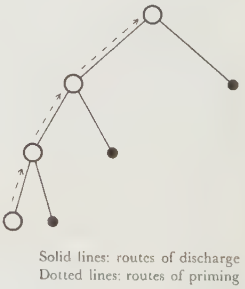
Solid lines: routes of discharge
Dotted lines: routes of priming

Fig. 11c

Of course these schemes intend to give no more than a simplified picture. There are a number of exceptions; e. g. in predators when growing up, hunger appears earlier than the hunting behaviour subordinate to it. (See Fig. 6. The reverse would indeed be biologically impossible, for a neonate requires food.) For the rest, however, type c seems to be the most common type of hierarchical organisation of instincts and motor mechanisms including consummatory as well as instrumental acts. In other words, there seems to be a kind of "priming route" guiding the tendency upwards from the bottom to the top of the hierarchy. The instincts seem to act as stepping stones along this route. Or, in the language of developmental physiology as enunciated by SPEMANN and others, an instinct may in some cases act as an "organiser" or "evocator" of the growth of its next-higher superordinate instinct, at least as far as priming is concerned. This might explain why the longest root is grown for the first-maturing branch. It still does not explain, however, why instincts must be primed at all.

Obviously more research will be needed before definite statements can be made on this aspect of hierarchy. Present evidence suggests an asymmetrical arrangement and maturation of hierarchical systems in man, in the cormorant and in some animals as dealt with in §§ 1 and 2 of this Chapter but in all these species we still know so little about the hierarchical system itself that we can venture only assumptions as to its developmental mechanisms. Considering that the essence of the ideas expounded here were launched by FREUD half a century ago as quoted above, one must admit that in the intervening time very little further scientific progress has been made on this point.

The concept of instinct re-evaluated

No doubt in future the discovery of priming in animals will seem to lead to deep encroachments on the concept of instinct. In order more fully to appreciate this, some broad lines must be drawn.

Once upon a time, everybody thought they could conceive a clear idea of the notion of instinct. Instinct simply meant innate behaviour. (At present the term "instinctive" as a synonym of "innate", still harks back to those happy days.) At that time, an instinct was supposed to be an innate linkage between an innate object, an innate reaction, an innate amount of nervous energy and an innate goal. It is true, there were some terminological differences between authors. On the afferent side of behaviour one might take one's choice between an innate stimulus object, sign stimulus, perceptual pattern, releasing mechanism or cognition; but in any event the object eliciting instinctive behaviour was supposed to be strictly and wholly innate. On the efferent side, whether it was called reflex, response, reaction, motor mechanism or erbkoordination, instinctive behaviour as such was considered to be entirely rigid. Similarly the amount of nervous energy eliciting or accompanying instinctive processes, called either impulse, drive, emotion, libido, reaction-specific energy or SAP, was conceived to be innate and physiologically determined. And, finally, the goal of instinctive behaviour was thought to be so much innate that it did not occur to anybody to doubt and discuss this point. Again, in those days, intelligence and and learning were considered as something of a quite separate nature, superimposed upon the solid and rigid foundation of instinct. An animal raised in complete isolation would, by definition, perform perfect and faultless instinctive behaviour after having attained maturity. (A complete experiment of this kind, however, has, at least in the higher vertebrates, never been made.) These ideas and theories may be called the *preformationist doctrine* of instinct.

A first breach in this doctrine was made early in this century when it became customary to compare an instinct with a steam-engine: the boiler and the fire under it (i. e. the drive and the amount of nervous energy) were considered to be innate structures, unaffected by the outer world, but the rest of the machinery (i. e. the eliciting object and the elicited reaction) was regarded as an inextricable intermingling of innate and acquired components. In particular, McDougall often used this analogy. The core of these ideas was that the sensory and motor patterns of instinct itself could be modified by experience, whereas the amount of drive and the goal could not. The word "modified", however, indicates that preformationism was essentially maintained.

At about the same time Freud went much further by stating that, in the initial stage of human development, instinctive drives are essentially neither elicited by a specific object nor directed towards a specific goal. According to his account, instincts or drives (Triebe) are essentially nothing more than unshaped and uncanalised amounts of nervous energy and even their sources were supposed to become largely aroused, stimulated and primed by depending upon (or leaning up against, or being anaclitic to) certain bodily functions or environmental occurrences. One might say that the boiler was still supposed to be innate but not the fire under it, nor the steam-pipe conveying the steam toward one or other part of the discharging machinery. The relation between innate and acquired components was no longer conceived as an intermingling but as an interlocking in one and the same developmental process. Broadly speaking this concept maintains that it is not the instincts that shape the individual's world but the world that shapes the instincts. The idea of instinct was converted into an abstract concept, indefinable and "nicht-anschaulich", something like a pluripotent system of "psychogenetic potencies" if such a term may be coined, analogous to the histogenetic and topogenetic potencies described in developmental physiology. Preformationism was thus, so to speak, replaced by the doctrine of epigenesis.

To be sure, Freud supposed the instincts to be largely preformed and predetermined by bodily conditions, erogenous zones, primal phantasies, hereditary factors, biological relations within the family and so on, but all these agents do not affect the notion of instinct as such; they are essentially only the *organisers* of instinct. Even the total amount of libido of all instincts together, including object-libido as well as ego-libido, was conceived by FREUD as a *variable* amount of energy (Ges. Werke V, p. 118; Stand. Ed. VII, p. 217). Virtually nothing was left at all of the previously generally assumed innateness of instinct.

In the course of the following years, namely the twenties and thirties, these and similar ideas gradually (but very slowly) penetrated among those students of animal behaviour who were so fortunate as to be able to avail themselves of the laboratory equipment and funds necessary for experimental work on the ontogeny of behaviour. The progress achieved in this direction can be assessed from the recent papers of HEBB (1953) and LEHRMAN (1954). From their argument no other conclusion is possible than that the idea of "innateness" usually associated with the concept of instinct must be considered out of date. One can only regret that so many workers in this particular field overshot their mark by throwing overboard the whole concept of instinct, merely through fear of its connotations.

On the European continent, on the other hand, the standard equipment of the average student of animal behaviour consisted of nothing more than a bicycle, a note-book, field-glasses and a hide made of old sacking. Thus field work and occasional zoo observations were practically the only sources of knowledge. In many cases the work was done exclusively during spare time and experimental work to any extent was out of the question. Consequently, it is not surprising that all these students studied "instinctive" behaviour without realising what they meant by this term. No behaviour other than "instinctive" behaviour could be conceived and the study of behaviour was considered identical to the study of instinct.

Nevertheless, among ethologists also, the idea of innateness of instincts gradually faded. The rediscovery of imprinting by HEINROTH and LORENZ made a breach in the innateness of the instinctive object. The rediscovery of hierarchy affected the contraposition of variable appetitive versus rigid consummatory behaviour and it also affected the assumed specificity of reaction-specific energies. Moreover, the rediscovery of priming led to discussion on the innateness of the amount of instinctive energies. Finally even the goal of instinctive behaviour, the supposedly rigid erbkoordination, has in some cases turned out to be for a large part a product of imprinting (THORPE 1954) or flash-learning (this paper p. 223). On another line of research the justification of the customary distinctions between "instinctive", "acquired" and "intelligent" patterns were brought into doubt. (KORTLANDT

1943; see also pp. 225, 226, 230, 231 and 241 in this paper.) From all this there can be no doubt that the concept of instinct is gradually merging into a formative principle, an abstract and indefinable organiser, or potency, or something similar in developmental psychology and physiology. A rapprochement toward similar ideas on this point expressed by such neurologists as von Monakow, or K. Goldstein, becomes apparent.

Downward priming

Having arrived at the end of this sub-chapter, the question may be raised whether there occurs also a *downward* priming process in hierarchical systems. This question is not easy to answer for it will be very difficult to distinguish downward priming from normal reinforcement in learning processes. One might even doubt whether it is possible to establish a criterion by means of which such a distinction can be made, or perhaps, in a bold mood, one might go so far as to state that downward priming is nothing other than a causal explanation of what until now has been called reinforcement. An example may illustrate this point.

As mentioned above, cattle-breeders sometimes try to cure a subnormal sex drive in bulls by means of a procedure which seems to be based upon an upward priming process. In these cases reinforcement is out of the question, for sexual gratification is attained by the bull not earlier than *after* the upward priming process has been realised. In these cases priming might be considered a type of learning without a reward. There also occurs, however, a number of cases in which cattle-breeders apply a reversed procedure: in these cases a bull which is unable to serve, due to a subnormal sex drive or to an insufficient extrusion, is trained for breeding by means of artificial ejaculation, combining a cow as a stimulus object and an artificial vagina as a consummatory object. In these cases no one is able to state whether the successful cure is to be attributed to the *stimulation* of the ejaculatory instinct, causing a downward priming of the mounting and extrusion instincts, or to the *rewarding* of the ejaculatory instinct, causing a reinforcement of mounting and extrusion according to the principles of conditioning theory. It seems doubtful, therefore, whether such a distinction can be useful. (See also Trautwein 1954.)

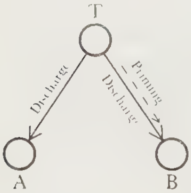

Fig. 12

Nevertheless, the problem may be approached from another angle. Fig. 12 will clarify this point. Take the case of a hierarchy consisting of a top-level instinct, called T and two subordinate instincts, A and B. During ontogeny A and B mature first and at a later age T matures. (No upward priming emanating from B is assumed.) Further, we will suppose that, due to environmental circumstances, either accidental or experimental, T is always satisfied exclusively by means of A. Or, in other words, B is redundant as an instrumental act in the service of T. Hence B is never reinforced by a rewarding of T. Now suppose further that the maturation of T appears to be followed by a gradual and lasting or permanent increase of the tendency of B and also that this increase appears to be unaffected by *later* fluctuations of the tendency of T. In this case downward priming would provide a possible causal explanation. An observational instance of this hypothetical case is suggested by Hunt (1941).

The question might be raised whether downward priming may provide an explanation for the observational facts according to which ascending development during ontogeny is accompanied by an increased variability of behaviour at a level just below the newly matured one and by a decreased variability at the lower levels. (See pp. 191 and 222.) This question cannot be answered yet.

It may be added that according to FREUD something like downward priming does occur (Ges. Werke V, p. 107; Stand. Ed. VII, p. 205) but in this case the exact nature of the phenomenon is too little known to justify a parallel between human and animal behaviour. For the rest, in the general framework of psychoanalytical as well as psychosomatic theories the reciprocity of connections (or vice-versa-principle, as it has been called with regard to displacement-activities) plays an essential role.

§ 4. THE PATHFINDING FUNCTION OF HIERARCHY

In the foregoing §§ of this Chapter, we have tried to find out what biological purpose hierarchy serves. Three main functions have been suggested: (1) formation of sensory and motor patterns by means of play exercise, (2) regeneration of acquired patterns by means of prevention of atrophy or by means of regression, (3) arousal of instincts by means of upward priming. In all these aspects we have found more or less definite evidence indicating that hierarchy of instincts bears some relation to the developmental processes which shape and reshape what is usually called "non-instinctive" (i. e. non-innate) behaviour. In other words, hierarchy of instincts is not so much an *organisation* of "*instinctive*" behaviour as an *organiser* of "*non-instinctive*" behaviour. Consequently, as a result of these findings, the demarcation line between "instinctive" patterns and "non-instinctive" patterns tends to disappear.

The peculiar nature of pre-rutting behaviour in deer

There exists yet a fourth category of behavioural phenomena which seems to be related to hierarchy and with regard to which the same statement given above can also be made. It is not yet quite clear, however, whether this category (which will be discussed now) must be considered a *separate* category, or whether it should be included under one of the three categories alluded to earlier in this Chapter. We will therefore start with some descriptions of behaviour before making any comment.

To begin with, the behaviour of male *Cervidae* preparatory to the rut will be considered.

The following account refers to Scottish red deer (*Cervus elaphus* L.) and has been taken from DARLING (1946, pp. 160–164). "The stags remain in companies until the velvet is shed. [About the third week of August.] At this time, a tendency for considerable movement among the stags is apparent. It is not altogether general, but new animals are noticed on the grounds; others which have been there all summer disappear. But there is no hint yet of the stags being in rut." (A recorded case of a circular movement observed in the second half of August and measuring at least 175 miles is mentioned by DARLING.) "A stag travelling in August and early September proceeds at a walk for the most part, but as the rut approaches his gait changes to a trot... During the week or two before the rut breaks, the stags appear to flock more than they have done for most of the summer. The bands move from end to end of their territories in the day and the observer cannot predict where they will be with the same assurance which he might have used a month before. At this time the stags are taking sly digs at each other with their antlers and the whole band occasionally indulges in a romp... The antlers are not used by the stag immediately they are clear of velvet, but as the rut approaches they are flourished in a neighbour's ribs in playful manner... In the week or two before the rut, the stags open up their wallows and roll in them once or twice each day... The rutting stag is black-brown after wallowing, and as I shall point out in another chapter, deer are more frightened of dark objects than of light ones... HINGSTON emphasizes the psychological value of the black-brown hair tufts or mane of mammals in fighting... The larynx of the stag develops during this period and he uses his roaring voice when he breaks into rut... September 20th is the traditional date for the rut to break in this area of the Scottish forests. Nutritional conditions during the summer make for some latitude." (Mounting up to October 1st according to DARLING's data. The quotations given above have been rearranged by the present writer in the proper chronological order apparent from DARLING's paper. See also loc. cit., pp. 79 and 99.)

From this description we may conclude that rutting behaviour in stags develops in the following sequence: (1) Random movements and roving far beyond the borders of territory. (2) Flocking, false fighting and wallowing, i. e. development of lower (or middle?) level sexual behaviour, accompanied by some roving inside the territorial borders. (3) Roaring, fighting and copulation, i. e. development of top-level sexual behaviour, accompanied by herding of hinds. In other words, at first a vague roving tendency emerges and thereafter roving decreases *in the same degree* as ascending development and integration proceeds.

Several aspects of this type of development have also been described by ALTMANN (1952, pp. 125–126) in her study of the wapiti, *Cervus canadensis nelsoni*. "During August the velvet is rubbed to shreds and the soft and probably sensitive antlers harden. This shedding of the velvet corresponds to the hormone level of the bulls according to WISLOCKI et al. (1947)... Gradually the behavior of rubbing the antler against trees is supplemented by beating each other and mock-fighting... In the last days of August the bull group at the Park was undergoing further changes. They still traveled together but the group was more spread out and more easily broken up... With the beginning of the second week in September, the bulls became bolder and were not easily disturbed. When a young bull passed a cow he raised his upper lip and ruffled his nose (domestic cattle fashion), a clear indication of sexual excitement or stimulation. The first bugling of bulls was heard on September 12th."

In ALTMANN's observational record no mention is made of phase (1), apparently because her wapitis were living in a fenced area of about 1500 acres owing to which extensive roving movements were impossible.

In English roe deer, phase (1) does regularly occur, as appears from TEGNER's statement (1951, p. 20): "The young are parted from their parents, when the doe is ready to give birth again and the buck departs on his wanderings, preparatory to the rut." (No further details are given by this author.)

A very romantic, but nevertheless excellent description of pre-rutting behaviour in the European elk (*Alces alces* L.) has been given by KAKIES (1936). The trustworthiness of his account is proved by what may perhaps be called the most remarkable photographic documentation ever produced on mammals living in the wild state. The following account pictures the behaviour of one prime bull, called "Elk" by KAKIES, which bull was observed throughout the seasons for several years. In this transliteration no attempt will be made to reproduce the original lyrical style; only the factual content will be extracted (loc. cit., pp. 28–30).

During the summer months Elk's antlers were steadily growing. In this period, on hot days Elk regularly bathed in the adjoining Baltic Sea in order to drive away annoying insects and to have a salty drink. During the night of 16th to 17th August the shedding of velvet was completed.

In the morning of 17th August, Elk browsed normally and nothing particular was noticed. It was a windy day so there were no insects. Nevertheless in the afternoon Elk went to the sea. This time, contrary to his previous habit, he walked up and down the beach before entering the water "as if gathering his strength". Then, after stepping into the sea, he adopted the sniffing attitude with his head raised on high. (German: flämen, or flehmen.) There was, however, no cow to be seen near or far, nor could there be any scent of a cow. (Normally, "flämen" is performed only if a cow on heat is present and further, in normal "flämen" the head is less raised. When this observation was made, a strong wind was blowing from the sea.) Then Elk walked some distance parallel to the waterline (quite contrary to his previous habits) and then went further into the sea and entered the actual breakers. He stood motionless for a moment and then a fusilade of kicking and jumping broke out. Like a thunder-bolt Elk dashed through the breakers, suddenly stopped and lashed the water with his feet, or jumped up with his four legs together and splashed and hurled the foam far around. He went back to the beach, shook himself, tossed his head, stamped his feet, re-entered the breakers and continued his furious raging and raving. According to KAKIES: "With every bound Elk spurned from him his previous easy life. The drive for browsing and chewing the cud which had ruled him hitherto has completely disappeared. His body bursts with energy and now this energy must need feel how all-powerful it is. It is a long time before Elk finally leaves the sea. He does not for a minute pause, nor is there any sign of fatigue; nor does he return to his territory as was his custom after his usual bathe. He sets off at a trot and travels southward mile after mile, his head poised high, his feet moving in wide, easy paces and the sand flying around his hoofs. The time has arrived in which love is far mightier than hunger." (Quotation, abridged and translated, from loc. cit., p. 30.)

It may be mentioned here that European elk bulls, in common with most male *Cervidae*, do not feed at all during the rutting period. From other data in KAKIES' book (pp. 36–38) it appears that Elk's rutting grounds were found about 25 miles southward. Such migrations in the pre-rutting and rutting period are regularly observed; on these occasions bulls may swim several miles, or perhaps even more (KAKIES, p. 47). Further, an important fact is that these migrations have been observed in prime bulls with excellent reproductive and fighting capacities and with a high degree of integration after breaking into rut, so we cannot suppose they were ousted by competitors. The explosive onset of rut in Elk bears out the finding made in cormorants, that a somewhat sudden eruption of the reproductive cycle involves very strong sexual, pair-forming, nesting and parental tendencies during the ensuing period. Here too, quality and quantity of behaviour are correlated to each other.

This description of pre-rutting behaviour in the European elk suggests that the sequence from phase (1) to phase (3) as discerned above must be considered incomplete so far. Before phase (1) a preceding phase of general, diffuse, undirected and uncanalised motor discharge, or overflow, or exuberance, or hybris, may occur. It seems as if the animal is unable to find in its stock of existing abilities a proper motor pattern, or even perhaps does not avail itself at all of such a pattern in order to discharge its pent-up internal "pressure" of "tension". Further, it seems as if, consequently, this pressure suddenly explodes into all the motor patterns which (in the given situation) are, so to speak, "nearest to hand". It seems, moreover, as if this outburst of diffuse libido *paves the way* for the *ensuing* canalisation and integration process which will *subsequently* cause the animal to pass through the forthcoming phases of integration as have been described by DARLING. In other words, it seems as if a so-called "instinctive" pattern of integrated behaviour (in this instance rutting behaviour) *is created* as a result of discharging an instinctive dim urge.

In this connection the reader will remember our finding (stated on p. 192) according to which, in the correlation between quantity and quality of behaviour, the strength of the tendency must be considered the primary factor and the degree of integration the secondary result in the causal chain. Furthermore, it will be remembered that flying co-ordination in the young cormorant is accomplished during the first 20 or 30 seconds of flying as a result of "flash-learning" (p. 223). Similar instances have shown that many so-called "acquired" behaviour patterns are actually innate patterns which, however, can be aroused or primed only by means of *external* stimuli (p. 225). Finally the reader will remember the vague symptoms of groping and reaching towards independence as described in the young cormorant in § 2 of this Chapter. And so in our argument we have now arrived at a very crucial point indeed.

At first glance it might seem possible that the behaviour of red deer, roe deer, American elk and European elk which has been described above, can be classified under one or other existing and generally recognised categories of behaviour. On further consideration, however, this possibility must be ruled out, at least if one wishes to account for all the facts.

One might suggest, for example, that migration simply belongs to rutting behaviour exactly as it does in birds or sticklebacks. This suggestion is negatived by the occurrence of circular migrations during the preparatory period, guiding the animal back to its original territory exactly when rut breaks; nor does such an explanation account for the decrease of inter-territorial movement as maturation progresses.

Or, one might suggest that we are here simply dealing with intention movements, appetitive behaviour, or something like that. We do know that intention movements and appetitive behaviour, when elicited, often show a marked sequence, starting with a diffuse motor unrest and ending up in very clear-cut and well-integrated behaviour patterns. The same sequence has even been experimentally elicited by Brügger (1943), Hess (1943) and Hess & Brügger (1943 a and b). As a matter of fact one of the most conspicuous characteristics by means of which instinctive behaviour can be distinguished from reflex behaviour is that the first always requires a preparatory interval during which the impulse is gradually set going and canalised. This interval, however, takes normally no more than a few seconds, or minutes, or at most hours, and it may be repeated every few seconds, minutes, hours, or days.[1] But in this §, on the contrary, we are dealing with a type of process which takes several weeks, or at least some days and which occurs only once a year. (It may be added that in man, similar processes with an identical symptomatic picture may take several years and occur only once in a life-time.) Further, intention movements and appetitive behaviour refer to the coming into operation of an impulse, whereas we are dealing with, at present, the coming into operation of a tendency (definitions on p. 189). Finally, intention movements and appetitive behaviour are so-called "instinctive", i. e. innate and identical in all members of one species, whereas pre-rutting behaviour is highly variable from one individual to another and seems to depend upon the absence as yet of a definite "instinctive" outlet for an instinctive impulse.

Or one might try to classify the behaviour in question under the heading of vacuum-activities, displacement-activities, or something similar. (E. g. Elk's assuming the "flämen" attitude might be considered vacuum "flämen", his lashing the sea some sort of aggression, and so on.) All such possible suggestions would, however, ignore the enormous variety of symptoms as well as the common characteristic features and tenor of all these symptoms in four different species. Vacuum-activities and displacement-activities are caused by specific and well-defined factors but here we find merely a *general* motor exuberance.

The same argument rules out a possible explanation by considering all these symptoms to be normal bottom-level behaviour, according to the principle of ascending maturation as expounded in Chapter II. It is exactly the multiformity of these symptoms which makes it impossible to fit them into the Procrustus bed of any circumscribed type of activities; although it must be said they are reminiscent of all existing types of generally recognised activities.

A hypothesis on "amoebic activities" or "ruptural behaviour"

It therefore seems that we shall have to reason the other way round: the wide variety of activities and motor unrest shown by *Cervidae* preparatory to the break of rut, lies at the common root of all more distinct types of activities which have been discerned as a result of diligent analytical research, and consequently this pre-rutting behaviour is reminiscent of all imaginably more distinct types of activities. Once again we come up against the "primary symbolic activities" in Portielje's terminology, or "amoebic activities", or "ruptural behaviour", as these symptoms have been called in § 2, p. 241. In these vague symptoms it would appear that a dim urge *searches for* its proper motor pattern and *tries to focus itself* at its goal. One might be reminded even of certain neurophysiological growth processes of nerve sprouts during ontogeny or organic regeneration, although such a resemblance may have only a deceptive appearance.

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[1] The difference between the reflex type and the instinct type of reaction may be illustrated here by quoting some experiments on homozygotic twin bulls taken by J. J. M. L. Crombach and W. de Rover (Research Group on the Behaviour of Domestic Animals, T.N.O.). In these experiments one sire was allowed to mount and ejaculate immediately after entering the serving stable, whereas the other one was restrained and prepared for 10 minutes before being allowed to serve. (In both cases artificial vaginas were used.) On the average, the number of live spermatozoa per ejaculate was found to be in the restrained and prepared sire 2,85 · as high as in the other one. Moreover, the general motility of the semen was found to be substantially higher. The experiments are still going on.

Some distinctions must, however, be made with regard to what has been discussed in § 2. There we were dealing with regenerative regression and in that context we gave special attention to those symptoms which were characterised by a progressive and regressive nature at the same time, or "reprogressive" symptoms as we then styled them. (3rd, 4th, and 5th developmental jump in the young cormorant.) Now, on the contrary, we are dealing especially with symptoms which are characterised *exclusively* by a progressive (or prospective) nature and in which no aspects of regression, reshuffling, reconditioning, etc., can be discerned. (2nd developmental jump in the young cormorant; see also pp. 238 and 241.) This distinction is particularly important because the regressive aspect points to the *existence* of an organisation of motor outlets which has become *obsolete* whereas the progressive aspect may indicate that an organisation of motor outlets is still in the course of *being shaped*, or is *non-existent* as yet. In other words, the variety, formlessness and multiformity shown in amoebic activities seems to be brought about because the development of a hierarchical system of outlets temporarily *lags behind* the development of its superordinate instinct, or source of energy. Further, it seems that this time-lag is due to the assumption that it is *precisely this outflow* of energy coming from the maturing superordinate instinct which has to *create* and *shape* its own hierarchical system of outlets. In yet other words, in our argument concerning amoebic activities, the concept of instinct tends to become a purely abstract formative principle, a creator of so-called "instinctive patterns" and an organiser of a so-called "instinctive" hierarchy.

With this tentative inference we have arrived at a very surprising point indeed. In the thirties Lorenz made an attempt to abolish the concept of instinct while maintaining the concept of instinctive pattern but here we are, so to speak, gradually coming to a position tending to abolish the concept of instinctive pattern while maintaining the concept of instinct! Now, in human psychology, surprise is an emotion which is closely related to doubt. And doubt may increase when we realise that, in a certain sense, our present tentative inference may seem to be exactly contradictory to all that has been said in Chapter II on ascending development.

Actually, however, such an apparent contradiction need not necessarily exist. In order to clarify this point, a scheme representing the principle of isolated development and ascending integration has been drawn up in Fig. 13. Three stages of organisation are taken to be passed through during the course of ontogeny. They are marked I, II and III, respectively.

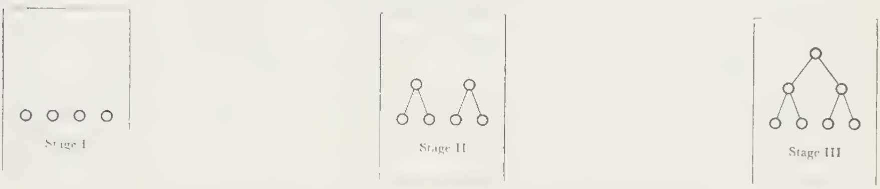

Fig. 13. Isolated development and ascending integration

It will now be clear that the principle of ascending integration as such stands quite apart from the question *how* integration is accomplished in the course of the *intermediary* phases of reorganisation *between* stages I, II, and III (i. e. the "mesoforms", NOVIKOFF). In Fig. 13 the transitional phases have been left open. Therefore a tentative suggestion with regard to the course of the reorganisation process has been drawn in Fig. 14. This suggestion is based on the evidence procured by *Cervidae*, cormorants, man and probably other species also, according to PORTIELJE.

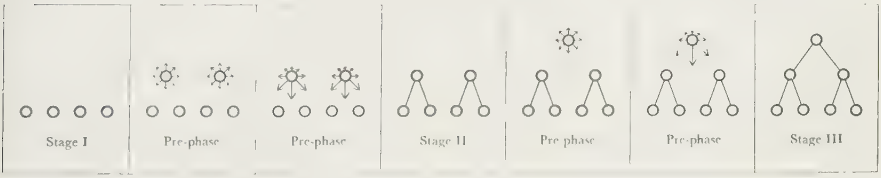

Fig. 14. The postulated full course of development

This schematic drawing demonstrates how, in the preparatory phase of the reorganisation process, a dim urge is assumed to send out its impulses (shown by arrows) at first indiscriminately to all the motor patterns which are, so to speak, "nearest to hand", in this way searching, feeling and reaching for its proper motor outlet, trying to focus itself on its "instinctive" goal, thereby causing a state of general motor restlessness and tension ("Sturm und Drang") in the animal. Further, in this scheme we see how, in the preparatory phase before reorganisation has been accomplished, a hierarchical system of outlets serving the newly maturing instinct is assumed to be non-existent as yet. Finally we are able to imagine how, in the course of time, these diffuse urges will gradually find and work out their ways toward their appropriate next-lower-level instincts, thereby creating and establishing a mature system of hierarchically organised instincts. One might even go so far as to imagine that a certain minimum amount of tendency is required in order that such a "working out" can be accomplished and maintained, in view of the phenomena described on pp. 190–196 and 240. (The process dealt with here should not be confused with conditioning, habit-formation and similar processes. There might be a common neurophysiological base underlying all such processes but this point lies outside the scope of this paper. No localisation theories are implied in Fig. 14. See also p. 179.)

Hypothesis critically examined

Hitherto the hypothesis expounded here with regard to the path-finding function of hierarchy contains two main features:

(1) It is assumed that a newly maturing instinct, in the very first phase of the maturational process, may still be unable to make use of its subordinate lower level instincts or motor mechanisms, although these subordinate instincts or motor mechanisms are potentially present or are even activated at the moment.

At first glance this assumption may seem rather strange. Actually, however, we have already come across several examples of this principle. On pp. 176 and 239 we have seen that most male cormorants at the age of 2 ½ to 3 months and at the age of about one year, are unable to use their building, inserting and quivering activities for the purpose of satisfying or discharging their appetite for a nest, although at that age these activities may be activated by a displaced impulse, and although at an *earlier* age the young bird did build, insert and quiver autochthonously (Fig. 5). Further, on pp. 184 we saw that a young cormorant is not able fully to employ its existing flying capacities in the service of its major appetites until at least 3 weeks after fledging (Fig. 7.) The same principle applies to other locomotory mechanisms. There even occur cases in which a young cormorant will allow itself to be pecked to death instead of simply fleeing. Finally, it may be remarked that a mature male cormorant in spring, during the first few days after his arrival in the breeding colony, is unable to perform any courtship display until he has chosen his nesting site. During these days he also shows a general restlessness and, moreover, the brightly shining colour of the orange or red patch at the corner of his mouth proves that the pair-forming tendency is already fully aroused in him (KORTLANDT 1949, pp. 33 and 80). All this evidence may suffice to show that our first assumption is less strange than it may seem at first glance and that it is even quite consistent with the general conception of hierarchy as expounded in this paper. Furthermore, it must be remembered that other authors too have often been struck by the fact that, in a great number of cases, an animal appears to be unable to use certain activities for certain goals although the same activities are easily employed for other goals. Moreover, the same phenomenon is also found in man.

(2) The second basic assumption in this hypothesis asserts that the subordinate instincts somehow attract or collect together the diffuse

impulses that irradiate from the newly maturing superordinate instinct, or point out the way to these impulses, and that ensuing impulses are subsequently led more easily in this direction, and so on in the course of time, until finally a smooth path leading from the higher to the lower instincts has become established. In other words, it is assumed that somehow the subsidiary instincts act as "stepping stones" in order to bridge the "physiological distance" separating the urge from its proper motor outlets and in order to create and establish a hierarchical system of instinctive connections. (No definite physiological interpretations are, however, implied.) To put it yet another way we seem to find here in ontogenetical development and maturation, some sort of "internalised" (or non-overt) trial-and-error learning process, which process may be conceived as at once a pathfinding and goalfinding process. In this process the subordinate instincts appear to act as something like an internal bait or intermediary reward.

At first glance, assumption (2) may seem nearly as strange as assumption (1). On further consideration, however, here too there appear to be several indications which make it look more plausible. In the first place the reader may be reminded of a statement by SUMNER (1934, p. 356) concerning the ontogeny of hunting behaviour in raptorial birds and already quoted earlier in this paper (p. 223): "Given an instinctive curiosity which impels the animal to follow moving objects, plus an appetite adapted to a diet of flesh, the rest naturally follows." The same principle applies to the development of drinking behaviour in newly-hatched chickens: an instinctive curiosity makes them peck at all glittering or otherwise conspicuous objects and, as a result, they discover the existence of water and *learn* to drink when thirsty (SPALDING 1873, p. 288, LLOYD MORGAN 1896.) If, however, chickens are kept without drink until three days or more after hatching, i.e. when the need of the organism will become sufficiently imperative, *instinctive* false drinking will ultimately appear, even if there is no water at all (BREED 1911, p. 76). Secondly, we may refer to our finding stated on p. 213 of this paper, viz. "As a rule (and perhaps always) A seems to serve as appetitive behaviour in the service of B. It looks as if Nature mistrusted appetitive behaviour and therefore has added to it some interim reward." Thirdly, in the cormorant, the neural connections leading the urge from the appetite for owning a nest to the building behaviour, seem partially to depend upon the degree of activation of the *tendency* of the appetites for bringing and inserting twigs, as has been indicated in Fig. 5, and this assumption finds support also when studying building behaviour in feminine and bisexual females, according to the characterological approach (KORTLANDT 1949, pp. 60 and 99). Fourthly, HEINROTH (1910, pp. 627–630) has given a detailed description demonstrating that domesticated geese (which are bad flyers and show a weak flying tendency) are characterised by a surprisingly low intelligence when solving, learning and remembering detour problems that can be solved only from the air, whereas their intelligence with regard to similar problems on the ground and on the surface of the water is very good. Tamed geese belonging to the wild race on the other hand, (which are reluctant walkers but eager flyers) easily solve, learn and remember detour problems from the air but appear to be very stupid when pinioned and thus faced with similar problems on the ground and on the water. Apparently it may be inferred that, at least in some instances, the *amount of tendency* belonging to the flying or walking patterns as *ends-in-*

themselves may *co-determine* the "intelligence" of the animal when employing these activities as *means-to-an-end.* (The term tendency as defined on p. 189.)[1] Fifthly, a case of the same tenor has been described by LORENZ (1937 a, p. 315). According to his account, a female canary had learned to use a specific nesting activity as an instrumental act (Werkzeugreaktion) in feeding behaviour, viz. to hold its food. This bird was, however, able to do so only during the physiological nesting period. When summer came it "lost" this ability. Sixthly, there is evidence that the "choice" of a particular displacement-activity by means of which a thwarted impulse is abreacted may be co-determined by the amount of (autochthonous) tendency in that particular activity[2]. It seems therefore that an instinct in which a strong tendency is present is more able to attract or catch up a thwarted impulse than a weaker instinct. Seventh, and finally, in this series of corroborations concerning assumption (2), it has been demonstrated that the peculiarity of the red-backed shrike (*Lanius collurio* L.) to impale insects on thorns in order to provide itself with a food store, contains a behaviour pattern which, under normal feeding conditions, is "acquired" by means of trial and error but which under "supernormal" (or "superoptimal") feeding conditions appears to be "innate" (KRAMER, quoted by LORENZ 1950, p. 237). Evidently in this instance the trial-and-error learning process which has been indicated as "pre-phase" in Fig. 14 becomes internalised if something like a tonic is administered whereas it remains externalised if this tonic is with-held. It seems tempting here to draw a comparison with the combination of roborative treatment and psychotherapy, as sometimes applied in human cases.

All this evidence may suffice to show that, at least in a number of instances, in addition to the principle of isolated development followed by ascending integration, we have to postulate something like a pathfinding function, exerted by the lower level instincts upon the higher level instincts during ontogeny and seasonal maturation, and causing

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[1] It need not be commented upon that we cannot attribute this effect to the impulse, or mood, or SAP to fly or to walk, for in that case the "intelligence" in question would not be a constant quantity. It will also need no comment that our inference does not apply to all motor patterns, for otherwise in Figs. 3–6 there would be only circles and no dots.

[2] On this point there has been some misunderstanding in literature. TINBERGEN (1952, p. 18) when discussing whether the state of activation of an instinct can influence the likelihood of its patterns being used as allochthonous outlets by another instinct, made the following statement: "It is striking that displacement activities are often innate movements which are frequently used in everyday life: eating, preening, etc... This seems to indicate that an animal is apt to use as outlets those patterns which for some reason offer least resistance... The only reliable evidence on this problem is brought forward by KORTLANDT (1940 c), and it seems to speak against such an influence. Fighting cormorants show displacement wing-flapping and 'gargling' (both derived from the sexual pattern) and 'nest-quivering' (derived from the nest-building pattern). Now although these activities, when autochthonously aroused, show a marked seasonal fluctuation, being frequent in spring but almost absent in winter, their use as an outlet during fighting remains the same throughout the year."

Actually, however, in a note inserted in the main text of the original paper, the present writer made the following statement (1940 c, Note 2, pp. 488–489, translated): "In spring 1939 I saw that, in the male, displacement wing-flapping occurs

(see cont. p. 263.)

the subordination of the lower levels to the higher ones by creating a hierarchical system of outlets. We do not know, of course, how this developmental mechanism works, nor do we know whether the tentative working hypothesis expounded above has reached the core of the problem. We cannot yet even make any definite statement as to the question whether such a developmental mechanism occurs in most instincts, or only in a minority of them; nor are we able to make any assumption on the question whether there may be any relation to the phenomenon of ascending variability discussed on p. 191. But anyhow, we may be pretty sure that there does exist at least some sort of such developmental mechanism, and can use it as a working hypothesis in order to tackle the problem.

Postscript

When the MS. of this Subchapter was nearly completed, the writer came across an outstanding and comprehensive study by T. M. FRENCH, entitled The Integration of Behavior, to be published in five volumes of which only Vols. I and II (1952, 1953) have yet appeared. The whole work will consist of a penetrating analysis of the acts and thoughts of one single person during two years of psychoanalytical treatment and this case-history is framed in general considerations dealing with the process of integration of behaviour and related topics. In his brilliant account FRENCH pays much attention to the biological mechanisms

(cont. note p. 262.)

more easily in the sexual period and that, in the female, it is strongly inhibited. Thus the strength of the sexual appetite does exert here an influence upon the release of displacement wing-flapping activated by the fighting impulse. The influence exerted by the appetite upon displacement wing-flapping is, however, much less than its influence upon the release of autochthonous wing-flapping. The last is completely inhibited in the female in the pair-forming period. With regard to other displacement activities belonging to the reproductive cycle, too, I believe I can now state that hormonal appetites exert a very small quantitive influence upon the inclination to spark over." In the Summary it was stated: "The tendency of a given impulse to spark over into a certain propensity disposition is *hardly* influenced at all by the strength of the (hormonal) appetite connected with the propensity disposition just mentioned." (loc. cit., p. 517).

Apparently TINBERGEN has overlooked these passages which are essential to the point under consideration. At present it may be added therefore that no doubt hormonal factors do stimulate the relative occurrence of allochthonous reproductive activities in fighting situations as compared to the occurrence of autochthonous fighting activities in these situations, but, for the rest, hormonal factors stimulate the relative occurrence of autochthonous reproductive activities still more. Consequently, in spring autochthonous activation of reproductive patterns predominates over allochthonous activation, whereas in autumn and winter the reverse is observed, at least if there is much occasion for fighting. More accurate data are, however, still needed.

underlying human behaviour including the achievements accomplished in this field by animal psychology, namely TOLMAN's "purposive behaviorism".

FRENCH's considerations are highly relevant to many problems dealt with in this paper and especially to the problem that has been suggested in this Subchapter. Nevertheless, the present writer has decided against including in this paper any detailed appraisal of FRENCH's findings. For one thing, as only two volumes have yet appeared, it would be somewhat premature to review them. Secondly, FRENCH's considerations are so profound that the present writer feels incompetent fully to survey all their implications. A prolonged study would be required for that.

§ 5. CONCLUSION

The concept of instinct re-evaluated again

Following the course of argument in this Chapter, we have gradually arrived at a position where hardly anything of the demarcation line between "instinct" and "non-instinct" seems to be left. In § 1 it has been concluded that "hierarchy of instincts serves to shape non-instinctive behaviour patterns during ontogenetical development" as a result of play exercise including the motor as well as the sensory aspect of behaviour (p. 231). In § 2 it has been shown, firstly, that hierarchy serves "to prevent or restrict atrophy and extinction of those functions which remain unused for a long time" (p. 232). And secondly, that (in regenerative regression) "regression and progression are aspects only of one and the same process by means of which a vague urge is trying to canalise its way and find its new shape" (p. 241). In § 3 we have seen that "an instinct may in some cases act as an organiser or evocator of the growth of its next-higher superordinate instinct" (p. 249). Finally in § 4 it has been suggested that "the outflow of energy coming from the maturing superordinate instinct has to create and shape its own hierarchical system of outlets. The concept of instinct tends to become a purely abstract formative principle, a creator of so-called 'instinctive' patterns and an organiser of a so-called 'instinctive' hierarchy" (p. 258). One can only pity the poor newcomer to the study of animal behaviour who must try to find his way in such a system of ideas! Once upon a time, long ago, an instinct could be simply defined as an innate system of units arranged in an innate hierarchy, each of which comprised at least an innate stimulus, an innate response, an innate goal and an innate quantity of nervous energy. Today, however, when surveying our science as a whole and taking into account the findings discussed here, none of these classic attributes of the concept of instinct seems to be left intact. Instead, the idea of *innate sensitive age-periods* comes more to the front.

Now, of course, one should not exaggerate. Nevertheless, it cannot be denied that we are gradually arriving at a conception of instinct in which all the clarity and concreteness of previous conceptions tend to disappear. In a certain sense the progressive aspect found in "amoebic activities" (or "ruptural behaviour" if the reader prefers this term) might be called "play"; for the element of "seriousness' characterising integrated behaviour is still lacking and this would imply that this type of behaviour must be included under § 1. In another sense, however, this type of behaviour might be called "regressive"; for in it the elementary patterns are coming to light again and in this respect the phenomenon should be dealt with in § 2. In still another sense, the pathfinding process might be considered as related to downward priming, which refers us to § 3. Moreover, in § 4, the pathfinding process has been conceived of as some sort of "internalised" trial-and-error learning process in which the subordinate instincts seem to act as something like an internal bait or reward. This last point, however, may in its turn lead us still further to an interesting concept launched by THORPE (1950) in which the current distinction between trial-and-error learning, latent learning, exploratory learning and insight learning is virtually eliminated and in which, moreover, the concept of insight is brought into relation with the concept of imprinting. Here we find that the investigator of "non-instinctive" behaviour and the investigator of "instinctive" behaviour are converging toward a rapprochement of views, tending to efface the old-time distinction between "instinct" and "non-instinct". Indeed, in so far as the pathfinding process in a hierarchical system of instincts may be conceived of as internalised trial-and-error learning, it will be difficult to distinguish this process from insight learning. On the other hand, however, in so far as the pathfinding process is determined by the pre-existing structure of as yet unconnected lower level instincts, it will be difficult to distinguish this process from such notions as arousal, flash-learning and priming. And, finally, there also exists a clear relation to the notion of sparking over, as usually applied with regard to displacement activities. On these points, preformationist and environmentalist doctrines seem to merge into each other.

Again, however, one should not exaggerate. What has been stated in this Chapter with regard to some instincts, in a number of cases, need not apply to all instincts everywhere. But however that may be, we can be pretty sure that future research on hierarchy will tend to disrupt the concept of instinct as well as the concept of learning. VON MONAKOW's concept of "instincts formatifs" comes in sight again. Links with experimental embryology may be expected. YERKES' curious definition (1948, p. 128): "Behaviour is structure in flux" might even become relevant.

There are a number of indications that in other fields of research on animal behaviour too, a trend toward reconciling the opposition of "instinct" and "non-instinct" becomes increasingly apparent. The orientation of European ethology toward fieldwork and ecology has led to the recognition that "Generally speaking all those bird species which in the wild state must adapt themselves to very variable circumstances are intelligent.... for them, intelligence has acquired survival value." (Translated from HEINROTH 1938, p. 150). Starting from this statement nothing can prevent us from conceiving of intelligence as something like a compound instinct. (See also BIERENS DE HAAN 1937, KORTLANDT 1943.) Other indications showing that the preformationist concept of instinct prevailing among ethologists until now is gradually disappearing, have been mentioned on p. 251. In this connection, research on imprinting should also be mentioned. It is true that ethologists have often defined their business as "the study of instinct", or "the study of instinctive behaviour", but such definitions usually contain a good deal of wishful thinking. In this case the peculiar aversion often found among ethologists to anything which is "learned" (in animals, at least) may easily explain the limitations of the definition.

Among our American colleagues on the other hand, the increasing interest in such fields as experimental neurosis and psychosis, psychosomatics, psychoanalysis, integration and social aspects of behaviour has laid open a very broad front of research as compared to the maze-running of rats which predominated in the past. No doubt this wider outlook will result in an increasing awareness of the impossibility of disentangling "innate" from "non-innate" behaviour. In this connection the following statement made by HEBB (1953) is symptomatic of the present state of affairs: "First studying the innate before studying learning is logically impossible... just as the learning theorist must know what growth processes do to behaviour before he can certainly say what learning does in the growing infant. Evidently we cannot separate the two tasks; they must be carried out together... I would not suggest for a moment that the problems in this area are unreal; I do suggest that they have been poorly stated, inasmuch as we cannot dichotomize behaviour into learned and unlearned, environmentally determined and hereditarily determined. I urge that there are not two kinds of control of behaviour, and that the term 'instinct', implying a mechanism or neural process independent of environmental factors, and distinct from the neural processes into which learning enters, is a completely misleading term and should be abandoned." (loc. cit., pp. 46-47).

From all these discussions one major lesson can be learned (a lesson which, since time immemorial, has had to be learned in every field of research but which has as often been forgotten since then): technical terms damage the delicate tissue of truth (RÜMKE 1953, p. 107). For this reason the present writer in his previous papers has always avoided using the word "instinct" and for the same reason one may expect that any attempt to re-evaluate the concept of instinct will meet with serious (and in a certain sense, justified) opposition springing from the older and established connotation of the word "instinct".

In this connection MASLOW's ideas (1943a, 1943b, 1948, 1954) deserve special attention. (See also pp. 187–188.) Of course, a general survey of them cannot be given here but the following quotation may illustrate the essential point: "Our main hypothesis is that human *urges* or *basic needs* alone may be innately "given" to at least some appreciable degree. The pertinent behavior or ability, cognition or affection need not also be innate, but may be (by our hypothesis) learned, canalized, or expressive. (Of course, many of man's *abilities* or *capacities* are strongly determined or made possible by heredity, e. g., color vision, ability to articulate, etc., but they are of no concern to us at this point.) This is to say that the hereditary component of basic needs may be seen as simple conative lack, tied to no intrinsic goal-achieving behavior, as blind, directionless demands, like FREUD's id-impulses... It was a severe mistake of both the instinctivists and their opponents to think in black-and-white, dichotomous terms instead of in terms of degree... The commonly accepted theory has been that instincts steadily drop out as we go higher in the phyletic scale, to be replaced by an adaptability based on a vastly improved ability to learn, to think, and to communicate. If we define an instinct, in lower animal style, as a complex of innately predetermined urge, readiness to perceive, instrumental behavior and skill, and goal object (and possibly even affective accompaniment if we could ever find a way of observing it), then this theory seems to be true. Among white rats we find by this definition a sexual instinct, a maternal instinct, and a feeding instinct (among other). In monkeys the maternal instinct remains, the feeding instinct is modified and modifiable, and the sexual instinct is gone, leaving behind only an instinctlike urge. The monkey has to learn to choose his sexual mate and has to learn to perform the sexual act efficiently. The human being has *none* of these (or any other) instincts left. The sexual and feeding urges remain (and perhaps even the maternal urge although very faintly), but instrumental behavior, skills, selective perception, and goal objects must be learned, mostly in the sense of canalization. He has no instincts, only instinct-remnants and instinct-anlagen. Side by side with this evolutionary development, there *may* be found another one, namely for the gradual appearance as we ascend the phyletic scale of new and "higher" urges, instinctoid in nature, i. e., predetermined in greater or lesser degree by the structure and functioning of the organism... Be it noted again that we speak here of instinctoid *impulses* or *urges* and *not* of predetermined instrumental behaviors, abilities or mode of gratification, i. e., *not* of instincts... Frustration of these needs is psychopathogenic, all clinicians agree... Clearly, therefore, the basic needs stand in a special psychological and biological status. There is something different about them. The burden of proof that they are *not* appreciably instinctoid rests upon anyone who denies this." (MASLOW 1954, pp. 330, 340, 342).

Bearing of the problem

A re-evaluation of our ideas on instinct as advocated here, leading to the recognition of an instinct as a rather tenuous and indefinable notion, viz. a formative and energetic principle, may at first glance appear to have little attraction for many biologists. Most of them have always been accustomed to regard an instinct as something like an organ or a mechanism, e. g. a compound reflex arc or a nervous centre. They will remember the confusion that arose in the past out of the concept of entelechy. Moreover, as a result of the nature of their scientific training, most biologists have become rather reluctant to occupy themselves with organic processes of which no organic substratum can be detected. In this respect the present situation has been exemplified by THORPE (1950) in the opening words of his paper read at the fourth Symposium held by the Society for Experimental Biology: "Individual self-preservation by means of accommodation to a changing and unstable environment is one of the most reliable criteria for distinguishing living from non-living. Yet there are few aspects of animal behaviour that have been more neglected by present-day zoologists than learning, ...which after all is one of the most important methods by which animals, and especially the "higher" animals, succeed in establishing a conservative equilibrium to change of external conditions."

It would seem that psychologically trained workers are more courageous in tackling such rather "ghostly" matters. Nevertheless, biologists too must tackle these and similar matters. These problems, how ever mysterious they may seem to be, should even be a challenge to biologists instead of being left only to psychologists. Psychology needs biology, and biology must play its part, for the following reasons.

Firstly, the problems on the border-line between instinct and non-instinct have such deep roots in such divergent fields of science (including e. g. psychiatry, ethnology, paedagogics) that they cannot possibly be surveyed by any single approach. A fortiori these problems cannot be left to any one group of specialised workers. In this paper, this state of affairs has been sufficiently demonstrated as far as the problem of hierarchy of instincts is involved and as far as this problem concerns *biological* workers. Thus we have seen how medical psychology in particular may contribute to the clarification of many specifically *biological* problems concerning hierarchy. No attempt was made, however, to demonstrate how biology, on the other hand, may contribute to the clarification of some essential problems of medical psychology or other sciences dealing particularly with man. Such an attempt would be out of place in a zoological journal. (Perhaps at a later date such a paper might be published elsewhere.) Nevertheless, it goes without saying that the problems centred around the concept of instinct occupy a key position in all sciences which are dealing with human nature. Consequently, these sciences cannot do without biological contributions to their frame of reference, and therefore biologists ought not to isolate themselves from human questions. There are several features of current psychoanalytical doctrines on which students of animal behaviour might give a relevant critique. (E. g. the relation between sexuality and aggression, SEWARD 1946; the relation between sexuality, tenderness and love, KORTLANDT 1949; etc.)

Secondly, these problems are too important to human welfare for any scientist of behaviour to ignore them. In order to illustrate this point (and at the same time in order to give a striking case of ascending integration, imprinting and pathfinding as observed in a human being), an instance may be quoted here, taken from one of the most remarkable of puberty biographies that has ever been published. It deals with a rather sinister type of boy, a boy who, many years later, became a well-known politician and whose career can be traced back as a natural outcome of his juvenile character and development. Indeed, all those features which later constituted the man, appear to have been already present in the boy. In a vivid account his biographer outlines how all these features became shaped as a result of the principle of isolated development and how they successively closed together as a result of ascending integration. Of course, in itself there is nothing unusual in this story: as we know such processes occur every day, everywhere. But in this particular case the point of interest is found in the decisive event when the pressure of the inner urge broke through the barriers, took its definite shape and created a human destiny. This event occurred when the boy was about seventeen years old.

Before this occurrence, according to his biographer, "there were in his life two years without any outwardly apparent purpose... Actually, however, this period of his life was full of restless activity... It is true, his activity was still rather unsystematic. In it no definite purpose or clear goal could be discerned. With unheard-of energy he only gathered impressions, experience and material to himself. What use he would make of it remained to be seen. At the moment he merely searched, here, there and everywhere." Then, one day, the boy and his friend (his later biographer) visited the opera "Rienzi", the story of which deals with a political career in ancient Rome. A man of humble origin named Rienzi, arises to liberate the Roman people from extortion and oppression by the ruling classes. He forms a national movement which gradually stirs the whole people. All power is given into his hands, he is proclaimed "people's protector" and "people's tribune"; but then, as is the natural course of political life, he is ultimately overthrown, and in his downfall he drags the Roman people to destruction with him. His last words are: "What! is this Rome? Misery! Unworthy to have this man; the last Roman curses you! Damned and exterminated be this town! Decay and perish, Rome! Such is the will of your people!" and then Rienzi perishes in his palace amidst the flames of blazing Rome. The curtain fell and both youngsters left the theatre. Then the biographer goes on as follows: "It was past midnight. My friend, his hands thrust into his coat pockets, silent and withdrawn, strode through the streets and out of the city... I asked him what he thought of the performance. He threw me a strange, almost hostile glance. 'Shut up!' he said

> brusquely... He looked almost sinister, and paler than ever... As if propelled by an invisible force he climbed up to the top of the neighbouring hill... And now he gripped both my hands and held them tight. He had never made such a gesture before. I felt from the grasp of his hands how deeply moved he was. His eyes were feverish with excitement. The words did not come smoothly from his mouth as they usually did, but rather erupted, hoarse and raucous... It was as if another being spoke out of his body, and moved him as much as it did me. It wasn't at all a case of a speaker being carried away by his own words. On the contrary; I rather felt as though he himself listened with astonishment and emotion to what burst forth from him with elementary force. I will not attempt to interpret this phenomenon, but it was a state of complete ecstacy and rapture, in which he transferred the character of Rienzi without even mentioning him as a model or example, with visionary power to the plane of his own ambitions. But it was more than a cheap adaptation. Indeed, the impact of the opera was rather a sheer external impulse which compelled him to speak. Like flood waters breaking their dykes, his words burst forth from him. He conjured up in grandiose, inspiring pictures his own future and that of his people. Hitherto I had been convinced that my friend wanted to become an artist, a painter, or perhaps an architect... Now he was talking of a mandate which, one day, he would receive from the people, to lead them out of servitude to the heights of freedom... He spoke of a special mission which one day would be entrusted to him... His words were followed by silence. We descended into the town. The clock struck three. We parted in front of my house. He shook hands with me, and I was astonished to see that he did not go in the direction of his home, but turned again towards the hills. 'Where are you going now?' I asked him, surprised. He replied briefly, 'I want to be alone.'"

The foregoing account has been quoted from KUBIZEK (1953, pp. 74–75 and 138–141; Eng. ed. 1954, pp. 64–66 and 70). Again, in itself there is nothing extraordinary or abnormal in such a passionate outburst in a boy at the age of puberty. On the contrary, such an outburst may be considered a quite normal mental accompaniment of the pathfinding processes which lead a man to find his destiny in life and love. Moreover, we have recognised a similar, quite normal symptomatic picture in decisive ages in cormorants and deer. In this particular case, however, not only a human destiny but also the world's fate for many decades was decided in a few hours, for this boy was Adolf Hitler, who in 1939 himself testified to the historical correctness of KUZIBEK's account of the episode, in the presence of witnesses, adding on that occasion "In that hour it began." We know now how it ended, and thus we are able to see his life and death as one great and elaborate imitation of Rienzi. This resemblance applies even to the imprecations on his nation embodied in many of his speeches, statements and orders, especially after the plot of 20th July 1944, ("If the German people was to be conquered in the struggle then it had been too weak to face the test of history, and was fit only for destruction"; address to the Gauleiters, August 1944), and further the resemblance is also found in several technical details of his suicide and funeral. (TREVOR-ROPER 1950, pp. 36, 53–58, 92, 158, 215–216.) No example is indeed more apt to illustrate the tremendous importance in human life of such pathfinding and imprinting processes as have been dealt with in this paper and therefore biologists too should play their part in the study of these processes, instead of being frightened by such human implications and evading them.

There is yet a third reason for which biologists should participate in the study of developmental dynamics underlying both human and animal behaviour, instead of devoting their efforts mainly to falsely assumed "instinctive", i. e. preformistically determined behaviour. At the present time, orthodox psychoanalytical doctrine as it was established by FREUD is rapidly growing out of date. The war and post-war needs have torn open the seclusion in which psychoanalysts previously practised their magic art. New lines of approach have been discovered by e. g. ALEXANDER, FRENCH, HORNEY, MASLOW, MASSERMAN, ROGERS and other American investigators, as well as by some scattered European workers. Owing to the opening of such fields as psychosomatics, "non-directive" counseling, social case work and, in Europe, "Daseinsanalyse", new prospects of therapeutic approach have emerged. At the same time old techniques and concepts are being reappraised. Moreover, apart from the progress made in medical and allied fields of psychology, the present-day expansion of sociology and other social sciences has given a fresh impetus to psychoanalysis and other sciences dealing with human nature. Recently the aim and programme of conflictology (a branch on the borderline of medical and non-medical psychology) has even been boldly defined as "the science of the nature and treatment of psychological disturbances of healthy men living in a disturbed society" (VAN DEN BERG, 1955). Furthermore, there is an increasing awareness that the classic Freudian doctrine is a typical product of fin de siècle society. The great problem of our time is no longer sex but aggression and fear. Owing to these and other trends, the classic Freudian doctrine is gradually becoming a somewhat old-fashioned biological introduction to newly opened fields of research, instead of a gospel, as was the case previously.

Of course, nobody will regret this state of affairs; but, as a matter of fact, in this new development and re-orientation of psychoanalysis towards the social sciences, biology today stands aloof. The number of workers who are sufficiently trained to be able to bridge the gap between both branches of science is too small for their voices to be adequately heard. Terminological misunderstanding between workers of different origin is steadily increasing. Students of animal behaviour, generally speaking, are so divided in schools and groups of different origin that they cannot see the real problems on the border-line, not to speak of solving these problems. Consequently, as a result of the social trend in psychology, the biological basis of human nature threatens to become a forgotten feature in the study of man. The image of man as seen by those who are studying mankind becomes increasingly distorted towards a purely sociological concept.

Given this state of affairs we can do no better than to quote the concluding sentence with which FREUD ended his "Three Essays on the Theory of Sexuality" (Ges. Werke V, p. 145; Stand. Ed. VII, p. 243). "The unsatisfactory conclusion, however, that emerges from these investigations of the disturbances of sexual life is that we know far too little of the biological processes constituting the essence of sexuality to be able to construct from our fragmentary information a theory adequate to the understanding alike of normal and of pathological conditions." These words were at that time a challenge to biologists but the challenge passed unheard. Fifty years have elapsed since then. It must be admitted that, in the intervening time, very little actual progress has been made on this point.

SUMMARY

In this paper an attempt is made to review thoroughly the present state of research on the problem of hierarchy of instincts, including its implications for the concept of instinct in general. Arising from this critical examination, many preconceived ideas hampering our insight into the working organisation of instincts are disclosed, several current criteria and notions of instinct are re-evaluated, and finally, some suggestions for future research are offered.

In Chapters I–III the scientific trends which in the past have led to the development of theories implying a hierarchical organisation of instincts are critically reviewed. In Chapter IV new prospects of research are envisaged.

Chapter I

In 1905 FREUD launched an elaborate theory on the hierarchy of instincts and its ontogenetical development, of which the following points are of special interest to biologists.

During the initial stage of their development, subordinate instinctive drives are on the whole neither elicited by a specific object nor directed towards a specific goal. In the beginning these urges only represent rather unshaped and uncanalised amounts of nervous energy. During the following phase all these subordinate instincts become conditioned to an object and they find a motor outlet or goal. Thus, strictly speaking, neither the objects nor the goals are assumed to be innate, although it is true they are in fact assumed to be largely predetermined by innate factors, biological conditions, etc. Different subordinate instincts mature, become conditioned and find their goals more or less independently of each other, and often at different ages, i. e. in different sensitive periods. (Principle of isolated development.) In later phases, subordinate instincts unite into larger wholes under the governance of higher level instincts which remain independent of each other for some time until, at a still later age, these instincts in their turn join together as components in a still higher unit of organisation, and so on. (Principle of ascending integration.) In these integrative processes the object and goal towards which a higher level instinct will be directed is

assumed to be for a large part built up by the characteristics of the objects and goals towards which the participating lower level instincts are directed owing to their previous history. Thus the organisation of behaviour is built up from the bottom, step by step. Periods of progress alternate with static periods, and this sequence is correlated to the main levels of instinct organisation. If, however, in this development the building stones appear not to fit each other, integration will fail and a developmental stagnation or fixation will follow. In such cases the controversial drives may continue to lead a more or less independent existence, or they may be converted into a neurosis.

Today, the main features of FREUD's theory of instinct as summarised above (especially the principles of hierarchy, isolated development and ascending integration) have found fairly general acceptance, both among psychoanalytical and non-psychoanalytical psychologists and psychiatrists. Parallel ideas and convergent evidence have been produced in other fields of research, such as neurology and child psychology (VON MONAKOW, CH. BÜHLER, MONTESSORI). The restricted validity of some counter-trends of thought and controversial ideas (COGHILL, WERNER, the dogma of wholism) has become recognised. Consequently the principles of hierarchy, isolated development and ascending integration are no longer a theory; they have become generally accepted facts, at least in modern developmental psychology of man.

Chapter II

The first author who recognised a hierarchical organisation of instincts (i. e. driving agents) in animals other than man seems to have been LLOYD MORGAN. At the same time, however, he aroused much confusion by using the word "instinct" in other connotations as well and consequently his ideas on hierarchy met with little response.

McDOUGALL and GROOS, although recognising the observational facts pointing to the occurrence of lower level instinctive behaviour (e. g. false hunting in satiated dogs) ultimately insisted on denying the existence of instincts lower than top-level and they interpreted lower level instinctive behaviour as "play", to be ascribed to a non-specific surplus of nervous energy. This rejection of the idea of hierarchy by these authors can be ascribed to the linkage of the objectivist concept of "instinct" with the subjectivist concept of "emotion" as implied in their theories, for it would appear that instincts are hierarchically organised whereas emotions are not. Apparently there is no specific link between instinct and emotion at all.

It is PORTIELJE's concept of "differentiation" of drives which has ultimately paved the way for the ideas on hierarchy of instincts devised afterwards by several of his compatriots. His emphasis on the Coghillian type of development, as well as his adherence to the McDOUGALL concept of instinct has, on the other hand, hampered him in recognising the full implications of the principle of hierarchy.

Enlarging on PORTIELJE's findings, the present writer developed an elaborate concept of hierarchy of instincts as a result of his investigations on cormorant behaviour. These results which were first published in a number of papers ranging from 1940 to 1953 are summarised, partly revised, re-evaluated and enlarged, in the present paper.

At first it is argued that a true hierarchy of instincts is essentially a hierarchy of so-called "appetites", or to be more precise, a hierarchy of goals or purposes towards which the animal appears to strive by means of a corresponding hierarchy of sets of appetitive behaviour, each of which is characterised by an adaptive variability of behaviour in such a way that the variations serve the corresponding purpose. According to the nature of the particular appetite, its "goal" may be either the performance of a consummatory act or the presence of a consummatory object or situation which causes the ending of a variable sequence or series of activities leading to this act, object or situation. In the cormorant these goals appear to be arranged on hierarchical levels such that the pursuit and attainment of a lower level goal may (or may not) be used as a means to an end in order to attain a higher level goal towards which the animal is striving. In other words, one and the same activity may at the same time represent a goal in itself, i. e. a consummatory act (serving its own level) as well as a means towards a superior goal, i. e. an instrumental act (serving its next higher level). If, owing to a natural or experimental situation, a superordinate appetite is satisfied in such a way that the accessory subordinate appetites are not also satisfied, the latter will continue to pursue their own goals and to seek their own satisfaction. Examples of hierarchical systems that were analysed in the cormorant are represented in Figs. 2–4. (Small dots in these Figs. do not indicate appetites but motor mechanisms which appear to be exclusively appetitive patterns and are never used as goals in themselves.)

During ontogeny and seasonal maturation the appetites (i. e. the pursued goals) belonging to one hierarchical system appear as a rule to mature and integrate successfully in a definite sequence, starting with the bottom-level and ending with the top-level, according to the principles of isolated development and ascending integration as described in Chapter I. No statement is possible as to whether "the" appetitive behaviour or "the" consummatory act matures first, for in the course of maturation, the process of ascending integration transforms initial "consummatory" behaviour (serving its own level) into subsequent "appetitive" behaviour (serving its next higher level). Examples of this type of development are represented in Figs. 5 and 6. (Fig. 6, however, also shows an exception from the normal sequence.) Locomotory functions also appear, as a rule, initially to grow and mature as independent patterns and goals in themselves, before they are gradually put at the service of the major instincts. An example is given in Fig. 7. The differentiative (or Coghillian) type of development on the other hand which is the counterpart of the ascending type, is rare in the cormorant.

In addition to this conception, it is assumed that in a hierarchical system each appetite at any level has its own innate releasing mechanism or choice of satisfying object, so that the bottom-level ones are least selective, the middle ones are more selective, and the top-level one is most selective; and furthermore, it is assumed that the innate object (or releasing sign stimulus) towards which a higher level appetite is directed is mainly composed of the characteristics of the innate objects (or stimuli) towards which its subordinate lower level appetites are directed. Consequently the increase of selectivity (or "differentiation" as it was called by PORTIELJE) which is observed during ontogeny and seasonal maturation must be attributed both to a shift in the level from which the main body of the motivation originates, as well as to the principle of ascending integration. If, however, after the completion of maturation, the top-level appetite is satisfied experimentally in such a way that at the same time a subordinate appetite remains unsatisfied, the unselective choice of object of the latter will come to light again.

The basic concept of hierarchy as outlined here appears broadly to co-incide with the developmental principles in man as described by FREUD, VON MONAKOW, CH. BÜHLER, etc., although actually this concept was conceived largely unaware of the latter. Moreover, independently of the present writer, convergent ideas indicating a hierarchy in the food-seeking behaviour of mammals and birds were suggested and experimentally confirmed by several American investigators. Enlarging upon their findings, MASLOW elaborated a general concept of hierarchy which holds that, as we go up the phylogenetic scale, innately maturing hierarchical systems appear to be substituted by hierarchical systems which are shaped by object finding, goal finding and ascending integration.

In this way MASLOW too built a bridge uniting the conceptions of animal psychology and psychoanalysis, but considering that he paid no attention to the ontogeny of the innate aspect of hierarchical systems, one might say that he failed to construct the middle span of this bridge. On this point the findings obtained in the cormorant demonstrate that, in the course of ontogeny and seasonal maturation, the intensity of the so-called "tendency" (i. e. the *average* strength of the drive, over a longer span of time, not to be confused with its *actual* strength) is correlated to (and probably determines) the hierarchical level of behaviour resulting from it, as shown by the degree of purposiveness, integration and canalisation, the selectivity of choice of object and the initiating of such processes as starting the reproductive cycle, settling down in a territory, falling in love with a mate, etc. More briefly, the average available quantity of drive determines both its average and its actual quality. Further, it appears that the zone of variability in behaviour ascends in the same degree as does the progress in maturation. During seasonal "dismaturation" (when the reproduction period is over) or in cases of ill-health or trauma, the whole sequence is reversed and purposiveness, integration, selectivity to objects and variability descend again to the levels that were observed previously. Apparently, therefore, ascending integration and descending disintegration are fundamentally identical processes which depend mainly on shifts in the degree of internal (hormonal) maturation, whereas learning plays at most only a minor role. This conclusion finds support when comparing resemblances and differences between special types of activities (e. g. intention-movements, displacement-activities, play, abreacting, etc.), and also when comparing differences between individual cormorants of divergent temperaments. Nevertheless the choice of object resulting from ascending integration appears also to be affected by previous conditioning exerted at the lower levels at an earlier age, for a mature cormorant when nesting prefers to settle at a site which resembles the type of landscape in which it grew up.

Chapter III

In the ethological branch of animal psychology, the idea of hierarchy was originally rejected by LORENZ who, in a somewhat dogmatic way, discarded the existence of any superordinate instincts or co-ordinating mechanisms higher than the bottom-level fixed action patterns (Erbkoordinationen) which at the same time were considered to be the only sources of internal motivation. The idea of hierarchy was, however, re-introduced when BAERENDS described in the female digger wasp a hierarchy of moods together with a corresponding hierarchy of appetitive behaviour patterns. His concept of hierarchy may be considered in many respects identical to that of the present writer, although the two concepts were conceived independently of each other.

In subsequent years, BAERENDS' concept was extended and re-modelled into a so-called "hierarchy of causal factors" by TINBERGEN who, at the same time, postulated a hierarchy of nervous centres underlying this hierarchy of causal factors. Actually, however, it can easily be demonstrated that neither a common component found in two (or more) sign stimuli eliciting different activities, nor even a common component in the internal drives activating different activities is in itself proof of the existence of a common nervous mechanism underlying these activities. (An example is given in Fig. 8.) Ultimately therefore, hierarchy is essentially not a matter of drives but of goals, i. e. co-ordinating and integrating factors which determine directiveness in behaviour, whereas TINBERGEN has interchanged the essential and the accidental features of hierarchy.

On further consideration TINBERGEN's misconception appears to be interwoven with the ethological doctrine according to which an instinct can be discharged and satisfied *exclusively* by means of a consummatory act, for this doctrine implies the recognition of an apparently "hierarchical" causal switch-board system for conducting impulses to their motor outlets while at the same time implying the rejection of any superordinate goals higher than the bottom-level, such as the appetites for food, for being paired, for owning a nest, for social group organisation, etc. In this respect TINBERGEN has still definitely maintained the rejection of hierarchy as originally formulated by LORENZ. Actually, however, there appears to be a wealth of facts disproving the doctrine which asserts that satisfaction is always attained by an act and never by an object or a situation. Consequently TINBERGEN's switch-board model cannot be held and hierarchy must be conceived as a hierarchy of co-ordinating and integrating factors corresponding with as many hierarchically arranged goals. Moreover, this conclusion is corroborated by neurophysiological evidence gathered by HESS, BRÜGGER, et al.

At the end of Chapter III the question is raised as to circumstances which have hindered ethologists from realising the full bearing of their findings on hierarchy and related phenomena. An explanation is offered by pointing to the peculiar nature of ethology as a scientific reform movement.

Chapter IV

In this Chapter an attempt is made to explore those aspects in the theory of hierarchy which until now have remained rather obscure. The question why hierarchy works as it does is chosen as a starting point.

§ 1

First, the formative function of hierarchy is considered. According to the theory of GROOS, young animals play in order to train and exercise their abilities before cases of emergency require full proficiency. Although experimental evidence is rather scanty, there appears to be a category of examples in which this theory explains the teleological efficiency or survival value of the principles of isolated development and ascending integration which guide ontogeny. Nevertheless, in these cases too, the question still remains: Why has Nature, so to speak, endowed the young animal with a set of innate drives to learn the skills it needs, instead of simply endowing it with a corresponding set of innate skills?

When surveying the animal kingdom as a whole, there appears to be a biological relation between the occurrence of juvenile play on the one hand and the required degree of variability, adaptability and complexity in adult behaviour, on the other. (In this connection a digression on the ontogeny of wildness and tameness in birds, mammals and man is included.) One might say, therefore, that the simpler types of machinery are innate, whereas the more complicated types of machinery are acquired as a result of experience in play combined with ascending integration. Neurophysiologists may try further to find out why acquired patterns should be biologically superior to innate patterns but anyhow it follows that, in one category of cases, hierarchy of instincts serves to shape so-called "non-instinctive" behaviour patterns during ontogenetical development.

§ 2

Having arrived at this point, the question may be raised why hierarchy continues to exist in adult life, albeit in a latent state. It appears that hierarchy exerts a twofold regenerative function.

Firstly, a hierarchy of tendencies correlated to the whole system of activities available to an animal will prevent atrophy and extinction of those functions which would otherwise, in certain circumstances, remain unused for a long time; and further it will prevent monotony and petrifaction of those functions which otherwise would be used in a stereotyped way. This point of view implies that the mere existence of a biologically valuable behavioural mechanism (either motor or sensory) will in itself provide an evolutionary force tending to develop a special instinct serving to activate and keep fit this mechanism during the vicissitudes of the individual's life. In this connection the existence of perceptual sub-instincts is argued.

Secondly, hierarchy continues to persist latently after completed integration in order to make possible regenerative regression by means of which a reconditioning, remodelling and reshuffling of the composing partial patterns of behaviour can be accomplished. In man this regenerative function plays an important role in the healing processes owing to which pathological fixations may be overcome; but curiously enough, in literature on animals other than man, hardly any indication pointing to the occurrence of this healthy type of regression can be found up till now. In the cormorant, however, symptoms of regenerative regression are very conspicuous in the preparatory phases preceding the third, fourth and fifth developmental jump belonging to the developmental sequence leading the young bird to individuation and independence. (In total, the whole process requires five jumps, each of which achieves a new organisational level of behaviour.) In each of these preparatory regressions the symptomatic picture is "reprogressive" (i. e. regressive and progressive at the same time), and "amoebic" (i. e. formless and multiform at the same time), and "ruptural" (i. e. lacking a definite texture). In these vague behavioural syndromes a new instinctive urge which has as yet no form, no object and no goal, appears to be trying to canalise its way and find its shape. When considering this process the distinction between "instinctive" and "non-instinctive" behaviour tends to fade.

In addition to these findings it is argued that, when considering the apparent relation between imprinting phenomena and hierarchy, in mammals and birds, there must exist certain remodelling, transforming, or regenerative agencies which exert their influence in the intermediate period between the imprinting of the lower levels and the maturation and integration of the higher levels. Up to now, however, nothing is known of these processes.

§ 3

Hitherto, hierarchy was regarded as a system in which impulses generated by superordinate instincts flow off downwards to subordinate instincts. Apart from this short-term one-way downward traffic of actual impulses, there is also fair evidence pointing to the occurrence of a long-term upward (or perhaps two-way) traffic of tendencies. (This term as defined in Chap. II.) In other words, a prolonged state of frequent external stimulation of a lower or middle level instinct may cause a lasting, or even permanent state of hyperactivation of the instinct next above it. ("Arousal" and "excitation" as defined by FREUD, "priming" as defined by VAN IERSEL.) The occurrence of this process may be restricted to a sensitive period during ontogeny or maturation. This means that in some cases an instinct may act as an organiser or evocator of the growth of its next-higher superordinate instinct. There even seem to be distinct priming routes leading from instinct to instinct and guiding the tendency upwards from the bottom to the top of the hierarchy. (Schemes are given in Figs. 10 and 11.) These findings imply a new breach in the preformationist doctrine of instinct.

§ 4

When studying the behaviour observed in deer preparatory to the onset of rut, a clear-cut developmental sequence appears to be passed through in a few days, or at most in a week or two. At first, a vague, diffuse, undirected and uncanalised motor discharge or exuberance emerges, which suggests that the newly maturing top-level instinct is not yet making use of its proper hierarchical system in order to discharge its pent-up internal pressure or tension. Subsequently, these vague, "amoebic" and "ruptural" symptoms of behaviour will gradually be canalised and they disappear in the same degree as ascending maturation and integration proceeds. It seems therefore, as if the originally diffuse discharge of a dim urge coming from the newly maturing superordinate instinct searches for its proper motor patterns, tries to focus itself on its goal and paves the way for the ensuing canalisation, until ultimately a fully-grown system of fixed outlets is established. The same type of process is found in the second developmental jump observed in the young cormorant. A scheme representing the postulated course (for which the term "pathfinding" is proposed) is shown in Fig. 14. The symptomatic picture of pathfinding processes differs from the "reprogressive" symptoms described in § 2 in that this time the symptoms are characterised exclusively by a progressive nature. This distinction is important because the regressive aspect points to the existence of an organisation of behaviour which has become obsolete, whereas the progressive aspect may indicate an organisation which is still being shaped, or non-existent as yet.

In the course of the pathfinding process as conceived above, the subordinate instincts seem to act as something like internal baits or stepping stones guiding some sort of non-overt trial-and-error learning process. The implications of this hypothesis are critically examined and its relation to the ideas on instinct and integration as expounded by French and Maslow is briefly mentioned. Here again, the concept of instinct tends to become a formative principle, a creator of so-called "instinctive" patterns and an organiser of so-called "instinctive" hierarchy.

§ 5

Following the course of the argument in §§ 1-4, it appears that the study of hierarchy leads into a no-man's land between "instinct" and "non-instinct". None of the classic attributes of the concept of instinct seems to be left intact. Instead, the ideas of "prospective potencies" and "sensitive periods" come more to the front. Preformationist and environmentalist doctrines are merging into each other. Links with experimental embryology are being established. Future research on hierarchy will tend further to disrupt the concept of instinct as well as the concept of learning. Yerkes' curious definition: "Behaviour is structure in flux" might even become relevant.

Finally the vital bearing of these scientific trends upon human welfare is illustrated by a striking case of imprinting, pathfinding and ascending integration as observed in a human being.

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COUNTERSHADING IN CATERPILLARS

AN ANALYSIS OF ITS ADAPTIVE SIGNIFICANCE

by

L. DE RUITER[1]

(Zoological Laboratory, University of Groningen)

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I. INTRODUCTION

Concealing coloration, or camouflage, in animals can be defined as follows: patterning which reduces the contrast between animal and environment to a level at which the probability that the animal will release inimical behaviour in other animals occurring in the same surroundings is smaller than it was at the preceding stage in the animal's individual or evolutionary history. Several of the animal's properties may contribute to its contrast with the environment (COTT, 1940). One of these is the gradation of light and shade which causes the body to appear lighter on its upper than on its lower parts when viewed in daylight in the open. Owing to this gradation, one can distinguish a solid body even when it is placed before a background whose colour and texture exactly match that of the object itself. Although, of course, the matter can be proved only by experiments, it seems highly probable that animals will also make use of this character in discerning objects in their environment. Hence, as COTT pointed out, it may be expected *a priori* that good camouflage will include the abolishment of shade. This can be brought about by a graded pigmentation which is darkest on the side the animal normally turns to the light, and lightest on the opposite side. At a suitable steepness of such a gradient, all parts of the body will reflect light of the same intensity.

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[1] The greater part of the observations were carried out at the Department of Zoology, Oxford, England. Some preliminary work was done at the Hulshorst station of the Zoological Laboratory of Leiden University. The results were worked out, and the paper written, in Groningen.

Now it is a striking fact that colour patterns of exactly this type are very common in many groups of animals, belonging to entirely different taxonomic and ecological categories. In view of the above, it seems reasonable to regard such pigmentation as an adaptation improving the camouflage of the animals concerned. POULTON (1888) was the first to describe an example of such coloration, *viz.* the chrysalis of *Apatura iris*, and to suggest that the pattern has concealing value. However, it was reserved for A. H. THAYER (1896a, b; 1902; 1911a, b; summary in G. H. THAYER, 1909) to grasp the widespread occurrence and the great functional importance of this type of graded pigmentation. THAYER introduced the terms "obliterative shading" and "counter shading" for the phenomenon. The latter, now commonly written in one word, has come into general use. THAYER's overenthusiastic generalisations have given rise to much justified criticism (*e.g.*, ROOSEVELT, 1911), but his opponents were unable to shake the fundamental principle of his theory.

Yet we must realize that what THAYER did when he enunciated his "law which underlies protective coloration" was to publish a hypothesis, based upon the observation that graded patterns are very common, and upon the surmise that what conceals an organism from the human eye will also hide it from other animals in its habitat. This assumption may or may not be valid. The issue can only be decided by watching the behaviour of these other animals.

However, the means so far employed in attempts to prove the functional value of countershading have been of a different nature. Deterred by the difficulties of behavioural observations, practically all workers have resorted to comparative studies. These revealed many correlations between the direction and steepness of pigmentation gradients on the one hand, and on the other hand the ecological, ethological and anatomical properties of the animals concerned. A review of these facts was given by Cott (1940). Taken as a group, these correlations can only be explained on the assumption that, in some respect or other, countershading has functional value. The only hypothesis so far advanced as to the nature of this function is that countershading has a concealing effect. Clearly, evidence of this sort will only permit general conclusions. Not even the largest amount of comparative data would enable us to affirm with complete certainty that in a given species countershading does indeed fulfill the function which, on the strength of these data, we believe it to have in most species. And, *a fortiori*, circumstantial evidence will never give us quantitative information as to the value of countershading. This can only be derived from observations on encounters between countershaded animals and their natural enemies.

In another respect, however, comparative studies are of great value. An important problem is whether countershading is an adaptation (for a definition see p. 319). This is by no means automatically solved if we can show that graded pigmentation has some functional value, because this might be a mere accident. The only way conclusively to prove the adaptive nature of countershading in an individual case would be to study its evolution while in progress. It is doubtful whether this will ever be possible. Therefore, we shall practically always have to content ourselves with indirect evidence on this point, and to obtain this we must turn to the comparative method. For that reason this method is an indispensable complement to the direct ethological and ecological study of single species.

In an outstanding contribution Süffert (1932) has shown that the larvae of Lepidoptera are excellent subjects for a comparative study of countershading. In addition, as will appear in chapter III, they are suitable for experiments with predators. These facts dictated the choice of caterpillars as the subjects of the present investigation.

I have in the first place tried to obtain further evidence for the adaptive nature of countershading through comparative work. Chapter II contains the results of these observations. Süffert's work has to a large extent plotted the course for further research in this field. I have attempted to strengthen the conclusions suggested by his studies by using a wider range of material, and by making a somewhat more complete analysis of the behaviour of the larvae. When striking the balance of our comparative data, I have tried to analyse the reasoning on which our conclusion is based in order to lessen the danger of neglecting possible alternatives.

My experiments with predators are discussed in chapter III. As far as I know, they are the first of their kind, for, surprising though this may seem in view of the fact that THAYER's theory was published almost sixty years ago, no data of this sort have yet been published apart from STEINIGER's short reference to his unsuccessful experiments (STEINIGER, 1938; see also p. 323 of the present paper).

The consideration that the success of an adaptive pattern depends upon the ethological organisation of the other animal for which the pattern is "meant" suggested another way of testing the functional value of countershading, *viz.* an analysis of this ethological organisation. Accordingly, I made some tests in order to ascertain whether the birds we used as predators do make use of shade as a character by which to identify an object (chapter IV). Although similar discrimination tests are often used in comparative psychology, their application to the problem of camouflage to my knowledge is a novel approach which may prove useful in the study of other types of concealing coloration.

Finally, chapter V is devoted to a discussion of the design of experiments on the survival value of camouflage, and the applicability of their results to some ethological and ecological problems.

I made some preliminary observations on the behaviour and structure of countershaded caterpillars in the summers of 1946 and 1947, but the greater part of the comparative work was done in 1952. Caterpillars are available only during a few months each summer, and ethological observations take much time. One season proved hardly sufficient for a study of this kind, which can be of any value only if a great number of species is investigated. Experiments with predators are exempt from the latter drawback, for here work with a single prey species can lead to conclusive results. However, this advantage is nullified by the difficulty of procuring large enough numbers of any single species, and by the fact that these tests are extremely time-consuming. For these reasons, our data showed many gaps when in 1952 I had to discontinue the investigation. Taken as a whole, however, they seem to lead to conclusions that are sufficiently based to justify the publication of this paper, though nobody can be more aware than its author that many points have not received sufficiently detailed treatment.

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II. INDIRECT EVIDENCE FOR THE ADAPTIVE NATURE OF COUNTERSHADING

A. THE NATURE OF THE EVIDENCE

This chapter is intended to show that the direction of the pigmentation gradient relative to the body is not the same in all countershaded caterpillars; that anatomically the gradient is carried by non-homologous organs; that nevertheless all investigated species in their natural environment turn their dark side to the light; that, however, this behaviour is due to reactions that may differ from species to species both on the receptor and on the effector side; that these reactions arise in development only at about the same stage at which countershading appears; and, finally, that the most important of these reactions are not found in non-countershaded species.

In fact, the only common feature of all countershaded caterpillars is their shade-less appearance. At the conclusion of this chapter we shall argue that this state of affairs can be understood only on the assumption that this shadelessness fulfills some function in the life of the larvae.

The body of facts needed for our argument cuts across the usual boundaries of anatomy, ethology, etc. Therefore, the best way to present the data is species by species. For reasons of space, these accounts will have to be brief, and entirely restricted to the information relevant to the problem of countershading. However, a more complete treatment of any single species would be well worth while, as I have tried to show in the case of *Endromis versicolora* (De Ruiter, 1954).

B. METHODS

A description of the material and methods employed must be given first. The greater part of the ethological observations were made on larvae reared from eggs obtained commercially.

For descriptions of the caterpillars we shall use Süffert's terminology, and speak of "normal countershading" when the gradient is dorsoventral, and the colour is palest on the belly, of "inverted countershading" when the gradient is dorsoventral with the back palest, and of "longitudinal countershading" when the gradient is parallel to the longitudinal axis of the body.

Caterpillars must be in very good health for observations on their behaviour to be reliable. I have taken all possible precautions to prevent overcrowding and excessive moisture, and to procure abundant fresh food. Yet virus disease proved a major problem in some species. We combated this by observing rigid sterility measures and by eliminating at once any culture that we suspected of being infected. This is a major cause of the gaps in our records. These precautions proved successful, as evidenced by the fact that we found no discrepancies between the results obtained with these caterpillars, and incidental observations made on wild specimens.

Feeding and resting are the main components of the behaviour of caterpillars. A small proportion of their time they spend in crawling, *e.g.*, from one spray of a food plant to another. When disturbed by the approach of an enemy, the camouflaged species under discussion freeze into immobility. When actually attacked, some of them may show a more or less specialised defensive behaviour. The latter, lying outside the field of camouflage, need not occupy us here.

It is generally known that the value of even the best camouflage is greatly reduced by movements that make the animal conspicuous. Hence, countershaded caterpillars would be best protected if they spent the day resting motionlessly in an appropriate environment, and were active only at night. There is some evidence (ESCHERICH, 1931; COTT, 1940; THOMAS, 1941; POULTON, 1932) that such behaviour prevails among caterpillars with other types of camouflage. In one case (*Charaxes jasius*), SÜFFERT (1932) made a similar observation on a countershaded species. However, I have not been able to show the existence of a diurnal rhythm in countershaded larvae in this or any other way. This may be due to our keeping the caterpillars in the laboratory. The question should therefore be regarded as open.

We have observed and analysed the behaviour of the caterpillars when feeding, resting and crawling. As already said there is a very constant relationship in nature between the attitude of a countershaded caterpillar and the position of the source of light. Obviously, this need not be due to an orientation to light itself. It can be brought about equally well by a reaction to any other environmental stimulus, the direction of which forms a sufficiently constant angle with that of the light. Two such factors come to mind, which on the twigs of the food plant might guide the caterpillars into the normal position, *viz.*, gravity and the structure of the plant. We have made some preliminary observations on the relative importance of these factors by offering them in different combinations to feeding and resting larvae, but we spent more time on the analysis of orientation in crawling caterpillars. Our motive for this emphasis on a seemingly unimportant activity was the fact that in most cases the position in which the caterpillar will feed or rest proved to be determined during locomotion (for instance, see the influence of a change in the direction of the light on *ocellata*, (p.295)), though sometimes other means of adjustment were found as well.

Caterpillars will go on crawling for greater lengths of time only on bare twigs. Therefore, we used such twigs in our experiments on crawling larvae. As might be expected, we never found any evidence that the structure of the plant could be a guiding factor on these twigs, so that only light and gravity remained as potential orienting stimuli. Now, in accordance with the common experience that caterpillars are negatively geotactic (GÖTZ, 1936), we found a general preference for the upper side of horizontal twigs. However, the larger the larva, and the thinner the twig, the more difficult it is for the animal to maintain itself on top. Caterpillars in the later instars often roll down passively to the underside, and are obliged to stay there. We never observed this passive obedience to the pull of gravity before the fourth instar in any species. Younger larvae found sufficient foothold even on thin twigs.

In order to separate the influences of geotaxis and passive obedience, we made parallel experiments on thin twigs (diameter 2–4 mm) and thick ones (diameter 6–10 mm). For the sake of comparability we used exactly similar twigs (dead, dry birch twigs of these standard diameters) in our tests with all species, although of course the diameter of the twigs of their normal food plants will vary, and will often be intermediate to our thin and thick twigs. Therefore, we made some additional observations on larvae on fresh twigs of their natural food plants for the purpose of determining in how far passive obedience to gravity there overrules geotaxis.

In order to assess the relative importance of light and gravity, we made the larvae crawl on horizontal twigs lighted from above, on horizontal twigs lighted from below, on vertical twigs lighted from one side, and, in one case *(ligustri)*, on horizontal twigs in diffuse light.

At intervals of at least half a minute, and often of one minute or more, we noted whether the larvae were crawling on the lighted side (dorsal light, scored as *d*) or the dark side of the twig (ventral light, scored as *v*). When a larva was just on the boundary of light and dark, we scored *o*.

On the following grounds we considered the interval between successive observations on one indiviudual long enough to ensure their mutual independence. (1) Even the young larvae were able to spiral round the twig at least once in this lapse of time. (2) Within the half minute intervals, frequent searching movements of the head of the larva could be observed[1], even if no change in position ensued, though in the latter case their extent tended to be smaller than when the larva reoriented itself. The conclusion seems justified that between any two observations each animal had made at least one and probably several active decisions whether or not to change its position.

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[1] Such movements were also observed in *Pieris brassicae* by COLLENETTE (1945), who suggested a similar interpretation.

The results of our observations are summarised in Table 1 (p. 297). As we shall see below, they form a sufficient basis for the generalisations made at the beginning of this chapter. However, there is considerable irregularity in the data we obtained. This is probably due to the fact that we were unable to control a number of factors influencing the behaviour of the larvae. For instance, apart from taking specimens in the same instar, and not using ones that were close to an ecdysis, we have not attempted to use larvae of the same age. Further, we had no means of controlling the temperature in the room where the tests were made, or of excluding vibrations set up in other parts of the building.

In all experiments made at Oxford we used the same source of light. This consisted of two electric bulbs (total power 160 W) mounted in one metal reflector. Two thick sheets of plate glass were used to screen off heat radiation. The distance between the light and the twigs was about 20 cm. Photometer readings showed that the light was fairly homogeneous along the bare twigs, and comparable in intensity to that among the leaves of a shrub on an overcast day. In the case of the leaved twigs used in some tests with feeding larvae, of course, the leaves cast patches of shadow on the twigs. Thermometer readings showed no measurable rise in temperature due to radiation from the lamps.

It should be kept in mind that all experiments were made at this one light intensity. Tests at different intensities on the same species might well give different results as regards the relative importance of the reactions to light and gravity. This, however, cannot affect our conclusion that the reactions to these stimuli are not the same in all species. Although we were aware of the importance of the problem (Fraenkel and Gunn, 1940; Süffert, 1932), we have, for lack of opportunity, not tried to distinguish between reactions to the direction and the intensity gradient of the light.

In the case of older larvae, only one caterpillar was placed on each twig in the tests with bare twigs. Of the younger instars, however, we used several specimens per twig, because we found that these did not or scarcely interfere with each other. In this case, we did not include in our notes the behaviour of larvae that were passing each other, or had just done so. Of course, larvae that were not moving were never taken into account. On reaching the free end of a twig, the caterpillars usually turned back after some groping around. At the other end, where the twig was held in a clamp, it was often necessary to make the larvae turn round by gentle touching with a soft brush.

For purposes of interpretation, it is desirable to express the data contained in Table 1 in a simpler form, based on the following considerations. If THAYER's hypothesis is correct, a countershaded caterpillar will benefit by its pattern if it sits with its dark side toward the light, but as soon as it turns its pale side to the light the distribution of its pigments will co-operate with the gradient in light intensity on the body instead of nullifying it. Shade will therefore be exaggerated, and the animal will be more conspicuous than if its pigment were evenly distributed (plates II and IV). In an intermediary position, a countershaded caterpillar will be approximately equally conspicuous as a plain one, and therefore run the same risks. Hence, the percentage excess of time spent in the "right" position may be taken as a measure of the adaptiveness of the behaviour of countershaded caterpillars. Our observations being independent, this is equal, within the limits of statistical error,to the difference D between the numbers of *dd* and *vv* scored in an experiment, expressed as a percentage of the total number of scores (including *oo*) made in that experiment:

$$D = \frac{\mathrm{N}_v - \mathrm{N}_d}{\mathrm{N}_{\text{total}}} \cdot 100$$

where N indicates the number of scores of a given type.

All species on wich we have made experiments have inverted countershading. Hence, their patterns have a cryptic effect only in the case of ventral illumination, so that for these species the adaptiveness of the behaviour increases with increasing D.

The above procedure involves the loss of some information contained in our original records (*e.g.*, the order in which *d* and *v* scores occur), which might be important for a more complete understanding of the caterpillars' orientation. However, the procedure is sufficient to shed some light on the question for which the tests were designed: are different mechanisms involved in the apparently similar orientations of different species of caterpillars? A special study will be necessary to solve the more fundamental problems raised by these orientations.

The reliability of a conclusion based upon comparative data increases with the number of species studied. For that reason, I shall not only discuss our own results in the following paragraph, but also mention some unpublished observations kindly put at my disposal by Dr. TH. ALBERDA, and give brief abstracts of SÜFFERT's accounts of a few species which I have not seen myself.

C. RESULTS

1. *Smerinthus ocellata* L. (Sphingidae; plate I, 1). In spite of the wide variation in the leaf colours of its food plants *(Salix, Prunus, Pyrus)*, the ground colour of the full grown larva of the Eyed Hawk always

exactly matches the green of the leaves among which it lives. This adjustment is due to an interesting special mechanism (Poulton, 1886, 1890), which, however, will not be discussed here. In addition, a perfect inverted countershading makes the larva appear as flat as the surrounding leaves. On each side the countershaded pattern is overlaid with seven slanting stripes. By their disruptive effect, these divert the eye of the observer from the outline of the caterpillar's body, making it more difficult to recognise. This disruptive effect of the stripes is enhanced by their being set off by a band of dark green along their dorsal edges. Dorsally, this band merges gradually into the lightening ground colour. At the ventral edge of the stripe, on the other hand, the ground colour lightens toward the stripe, so that the boundary between ground colour and stripe is hardly visible. Owing to this arrangement, the stripe suggests a ridge with shadow behind it. It is therefore very similar to a slightly prominent vein on the underside of a leaf. The patterning of these stripes is the logical counterpart of countershading, because it suggests relief where none exists. For cases of this sort, which are fairly common (Schwanwitsch, 1938), Cott (1940) has introduced the term "pictorial relief".

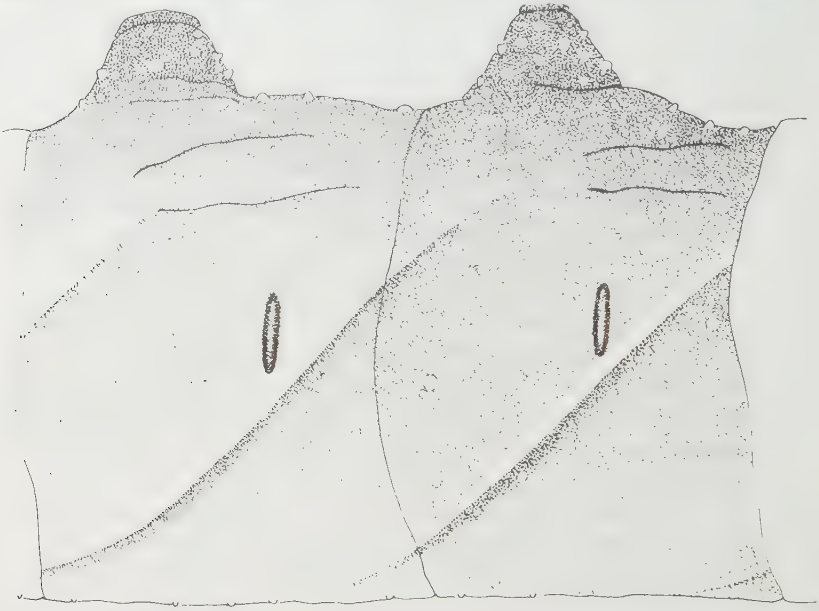

Fig. 1. *Smerinthus ocellata* L. The pigmentation of the 6th and 7th abdominal segments of the larva pictured in Plate 1, 1 (somewhat schematised). The larva is seen here in diffuse light, so that there is no shade. In reality, the gradients are somewhat steeper.

Dissection showed that almost the complete colour pattern (fig. 1) of

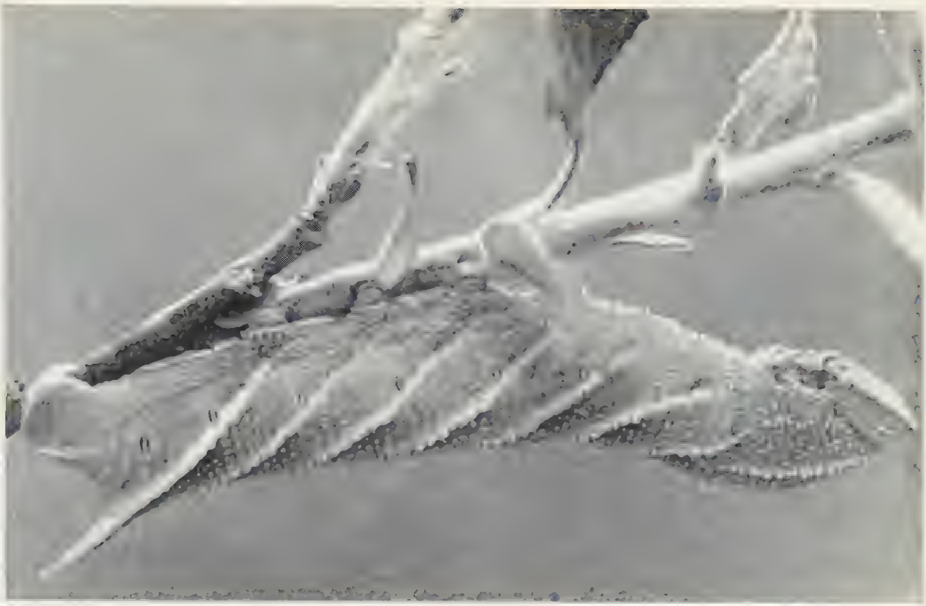

Plate I, 1. *Smerinthus ocellata* L. Full grown larva in resting attitude on *Salix repens* under natural circumstances. Note the absence of shade on the cylindrical body, and the pictorial relief of the slanting stripes, which are *not* prominent. Compare with fig. 1. (Photograph by Prof. Dr. N. Tinbergen.)

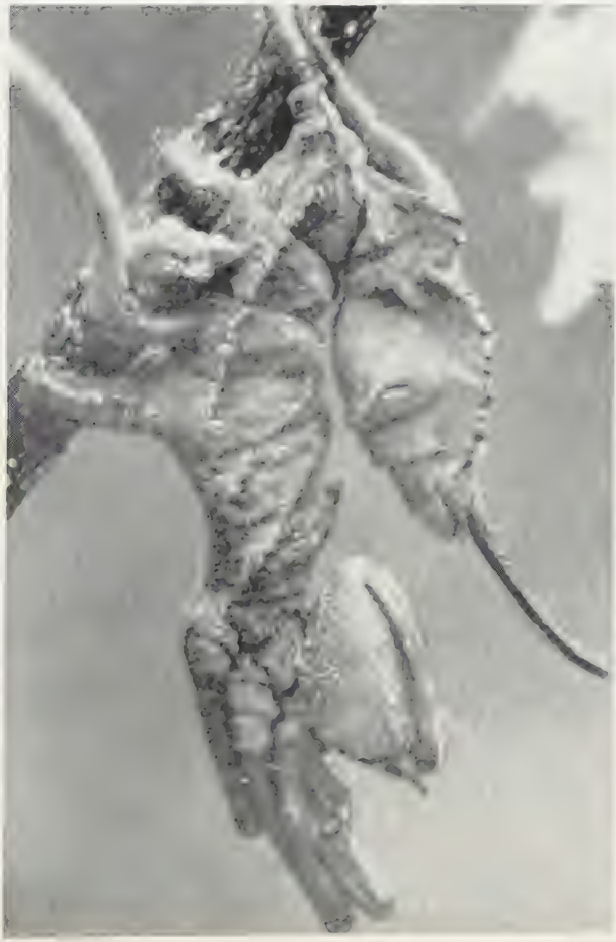

Plate I, 2. *Stauropus fagi* L. Full grown larva in resting attitude under natural circumstances. (Photograph by Prof. Dr. N. Tinbergen.)

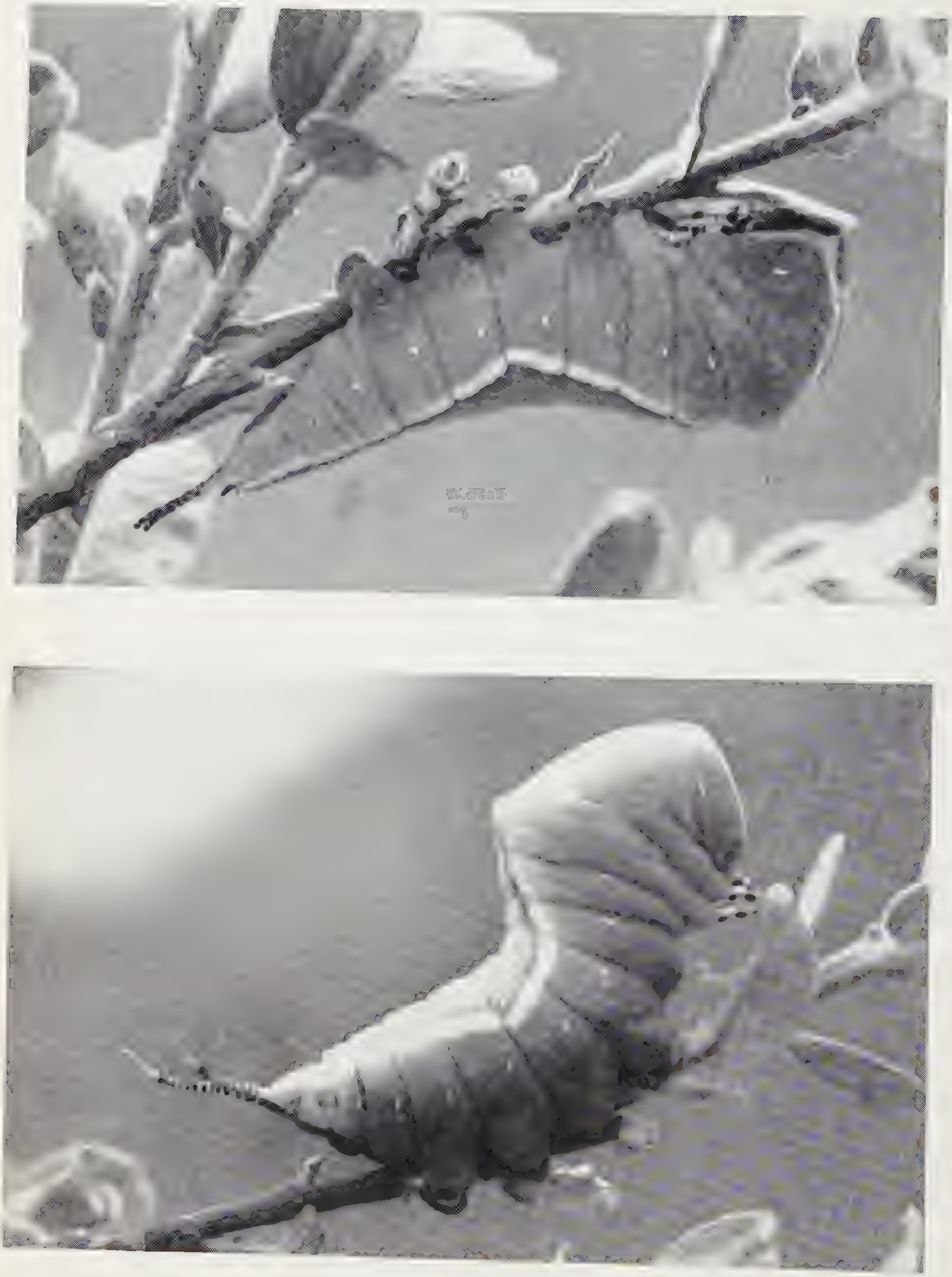

Plate II. *Cerura vinula* L. Full grown larva under natural circumstances, in natural attitude (above) and inverted (below). The two pictures were taken in immediate succession, under exactly the same conditions of light, etc. (Photographs by Prof. Dr. N. Tinbergen).

the full grown Eyed Hawk larva is located in the hypodermis. This is dark green ventrally, but grades over the sides into pure white on the midback. It also carries the slanting stripes in pure white, set off with dark green dorsally. Of the other organs, the cuticle is the most important. Its colour may vary from yellowish green (in pure green specimens) to practically colourless (in greyish green ones). Apparently this is the major factor in the minute adjustment of the ground colour to the green of the food plant, as I did not notice any clear difference between the hypodermes of very different larvae. In addition, the cuticle carries the tubercles which in *ocellata* larvae living on *Salix repens* heighten the resemblance between caterpillar and leaves by simulating the down covering the latter. The cuticle is not countershaded. Blood and gut are dark green, but their removal does not influence the appearance of the larva. The fat body is pure white. Lying dorsally to the gut, it may be of some importance as a screen between the dark gut and the very light dorsal regions.

In the younger instars, the pattern of the full-grown larva develops gradually. The stripes with their pictorial relief, and the inverted countershading appear in the course of the first and second instars, but do not begin really to influence the appearance of the caterpillar until the beginning of the third. It is interesting that at the same time the white subdorsals disappear from the abdomen. In the first two instars, these two stripes stretch over the full length of the body. From the third instar onwards, however, they are restricted to the thorax. In the larva's resting attitude, the well known Sphinx posture, they are then parallel to the slanting stripes on the abdomen, and fulfill an analogous function.

The following aspects of the behaviour of the Eyed Hawk larvae are relevant to our problem. In the field, the first three instars are practically always found on the underside of the leaves of their food plant. In the fourth instar, the larvae move to the twigs. The time at which this shift takes place is partly determined by the size of the leaves. On trees with very large leaves, even some fifth instar larvae may be found on the underside of the leaves. However, this is unusual.

On the twigs, the larvae always turn their ventral side to the light. The resting attitude is the entirely stereotyped Sphinx posture. When feeding, the larvae obviously assume somewhat varying attitudes.

Even in the field it can easily be shown on a sunny day with the aid of a small mirror that light is the main stimulus for the orientation of the larvae. If we screen off the direct rays of the sun, and give reflected light from another angle, the larva will readjust its position by crawling so that it again turns its ventral side to the light, no matter from which direction this comes. In crawling caterpillars, this reaction is almost instantaneous, but in feeding specimens it may be delayed for about two minutes, and in resting larvae for five minutes and more.

The results of our experiments on the orientation of crawling Eyed Hawk caterpillars have been summarized according to the method outlined above (p. 293) in fig. 2. There is considerable variation in the diameter of the leaved sprays of willows, but on the whole they may be more like the thin twigs used by us than like the thick ones. The first point to be noted is that on our thin twigs, lighted from above, *i.e.* under "natural" circumstances, there is a complete change in the behaviour of the larvae in the course of their lives (fig. 2, graph 1). At first, *D* is strongly negative, but it later becomes highly positive. That is to say that in the final instars the caterpillars' behaviour is in good harmony with the countershaded pattern.

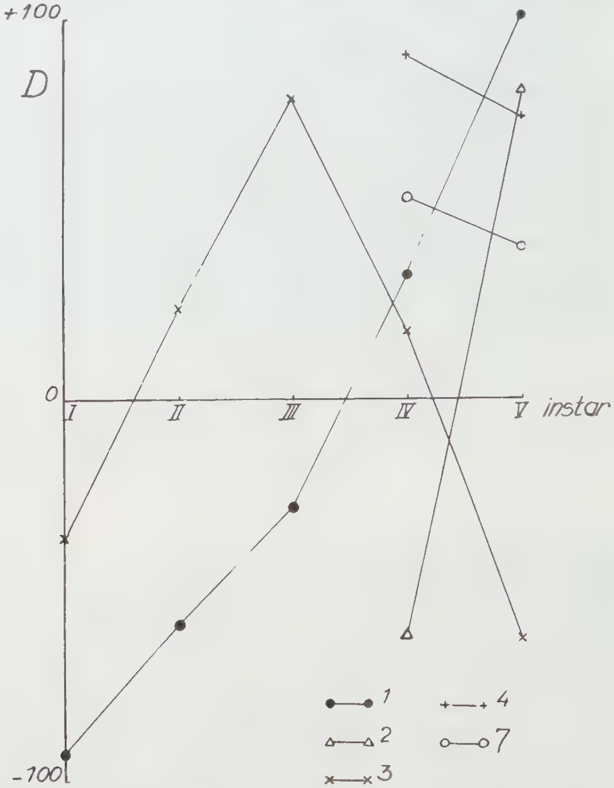

Fig. 2. *Smerinthus ocellata* L. Experiments on the orientation of larvae crawling on bare twigs. Abscissa: instars, ordinate: percentage excess of time spent in ventral or dorsal illumination (positive and negative values of *D*, respectively).
1: thin horizontal twigs, lighted from above; 2: thick horizontal twigs, lighted from above; 3: thin horizontal twigs, lighted from below; 4: thick horizontal twigs, lighted from below; 7: vertical twigs, lighted from one side.

TABLE I

Instar	Type of expt.[1]	Number of larvae used	Number of scores *dd*	 *vv*	 *oo*	*D*
Smerinthus ocellata L.						
I	1	5	233	0	17	—93
	3	5	135	46	67	—37
II	1	8	295	62	43	—58
	3	8	115	212	73	+24
III	1	8	97	40	63	—29
	3	8	6	163	31	+79
IV	1	5	30	65	11	+33
	2	14	257	47	34	—62
	3	4	26	44	30	+18
	4	4	3	95	4	+90
	7	4	16	69	15	+53
V	1	4	0	47	0	+100
	2	3	1	26	4	+81
	3	?	45	5	14	—63
	4	5	3	33	5	+73
	7	9	30	98	41	+41
Laothoe populi L.						
I	1	5	206	14	30	—77
	3	5	129	48	73	—32
II	1	8	337	22	41	—79
	3	8	79	234	87	+39
III	1	4	115	20	25	—59
	3	4	18	67	15	+49
IV	1	4	81	56	23	—16
	3	4	16	56	28	+40
V	1	8	30	80	19	+39
	2	6	91	4	18	—77
	3	8	77	23	10	—49
	4	5	2	75	18	+77
	7	6	45	25	18	—23
Mimas tiliae L.						
I	1	10	240	14	46	—75
	3	10	183	69	48	—38
Sphinx ligustri L.						
I	1	10	245	15	40	—77
	2	8	302	13	8	—90
	3	8	165	40	35	—52
	4	8	185	46	64	—47
	5[2]	8	264	44	21	—67
	6[2]	8	210	88	51	—35
	7	16	429	74	59	—63

Instar	Type of expt.[1]	Number of larvae used	Number of scores			
			dd	*vv*	*oo*	*D*
II	1	8	235	1	14	—94
	2	8	316	22	5	—86
	3	8	121	136	43	+5
	4	8	127	57	56	—29
	5	8	290	21	23	—81
	6	8	299	15	17	—86
	7	16	519	34	45	—81
III	1	6	132	68	50	—26
	2	8	281	12	14	—88
	3	8	144	73	23	—30
	4	16	330	179	91	—25
	5	8	275	49	16	—67
	6	4	62	23	16	—38
	7	14	344	77	37	—58
IV	1	5	7	109	9	+81
	2	4	71	25	12	—43
	3	4	77	14	11	—61
	4	8	160	114	32	—15
	5	4	42	77	8	+28
	6	4	71	21	13	—48
	7	8	155	19	47	—61
V	1	4	0	99	1	+99
	2	4	95	1	6	—92
	3	4	100	0	0	—100
	4	4	30	68	7	+36
	5	4	1	102	2	+96
	6	4	72	29	4	—41
	7	8	93	54	56	—19
			Cerura vinula L.			
I	1	9	247	7	16	—90
	3	10	184	62	54	—41
II	1	8	335	20	45	—79
	3	8	283	45	72	—60
III	1	8	373	1	26	—93
	3	8	175	73	72	—32
IV	1	4	152	24	24	—64
	2	4	172	20	8	—76
	3	4	67	26	27	—34
	4	4	42	50	28	+7
	7	7	100	24	44	—45
V	1	4	8	32	6	+52
	2	4	52	9	7	—63
	3	4	56	3	10	—77
	4	4	38	30	23	—9
	7	8	54	29	37	—21

Instar	Type of expt.[1]	Number of larvae used	Number of scores *dd*	*vv*	*oo*	*D*
Notodonta ziczac L.						
I	1	8	349	5	46	—86
	3	8	104	14	42	—56
V	1	4	4	92	11	+82
	2	4	62	5	34	—56
Stauropus fagi L.						
II	2	6	288	2	10	—95
III	2	5	148	4	8	—90
	3	5	5	114	44	+67
IV	2	5	95	0	5	—95
	4	5	0	96	5	+95
V	2	2	18	3	1	—68
	3	3	16	0	0	—100
	4	3	1	15	0	+95
Endromis versicolora L.						
I	2	8	281	0	39	—88
	4	8	209	39	72	—53
	7	6	155	4	21	—84
II	2	8	290	2	28	—90
	4	8	250	12	58	—75
	7	8	270	6	44	—83
III	2	2	80	0	0	—100
	4	8	150	66	104	—26
IV	2	5	93	1	5	—93
	4	5	51	18	29	—34
V	2	4	40	0	0	—100
	4	?	84	53	63	—16
	7	2	69	6	25	—63

[1] 1: thin horizontal twigs, lighted from above
2: thick horizontal twigs, lighted from above
3: thin horizontal twigs, lighted from below
4: thick horizontal twigs, lighted from below
5: thin horizontal twigs in diffuse light
6: thick horizontal twigs in diffuse light
7: vertical twigs, lighted from one side

[2] *d*: larva on upper side of twig
v: larva on lower side of twig

The shift from negative to positive values of *D* takes place about the time when countershading begins to be an important factor in the appearance of the larvae. On thick twigs, lighted from above, the change takes place somewhat later (fig. 2, graph 2). Hence, the fact that the larger larvae cannot maintain themselves very well on the upper side of the thin twigs undoubtedly plays a role in the adjustment of their behaviour to their pattern. Yet this is not the only cause of the strongly positive value of *D* in the full grown larva. This is largely due to a reaction to light itself, as evidenced, *e.g.*, by fig. 2, graph 7 which shows a strong preference for ventral light in older larvae crawling on a vertical twig, where gravity cannot play a role as an orienting factor.

Yet, in the earlier instars, there is a strong preference for dorsal light. It is noteworthy that the sign of the phototaxis changes just about the time at which the graded pattern reaches its completion. This can be seen from graphs 1 and 3 in fig. 2 in the following way. In our experiments we combined the various orienting factors in different ways. Now we do not know the rules according to which the different factors co-operate in giving *D* the value belonging to a given combination of stimuli. However, the assumption seems justified that the sign of the contribution to *D* of a given stimulus will always be the same as long as the direction of this stimulus relative to that of the light is constant. Now on a given instar of a species we can make two different experiments, using the same pair of orienting factors in both tests, but offering them in one combination in one experiment, and in a diametrically opposite combination in the other (their directions being parallel in one case, and opposite in the other). The absolute value $|D|$ will then be largest in that experiment of the two in which the two factors co-operate. The sign of the contribution of each factor can be concluded from the sign of *D* when it reaches its maximum absolute value.

Thus, in fig. 2 the comparison of graphs 1 and 3 shows that in the first instar orientation to light and gravity co-operate on the horizontal twig lighted from above. The fact that *D* in this case is negative, leads to the conclusion that there is a preference for dorsal light and for the upper side of the twig. In III, however, light and gravity co-operate when the twig is lighted from below, resulting in a positive *D*. In other words, the caterpillars still prefer the upper side of the twig, but phototaxis has changed to a preference for ventral light. In IV and V such an analysis is no longer possible in tests with thin twigs, as passive obedience to gravity here plays a role as well.

On twigs that offer a sufficient foothold, however, the caterpillars prefer the upper side throughout their larval lives. For the fourth and fifth instars this can be seen from the comparison of graphs 4 and 7, or of graphs 1 and 2 (fig. 2). For instance, in graph 7, where only light can influence the orientation, *D* has a smaller value than in graph 4, where negative geotaxis also contributes its share. Only the fact that graph 4 falls slightly below 2 in V does not agree with this interpretation. However, this discrepancy, and the decrease in 4 and 7 from IV to v are probably due to the fact that we used caterpillars too near pupation for experiments 4 and 7 in v. The reactions of caterpillars are known to change about that time (SÜFFERT and GÖTZ, 1936). For experiments 1, 2 and 3 in v, we used less advanced larvae.

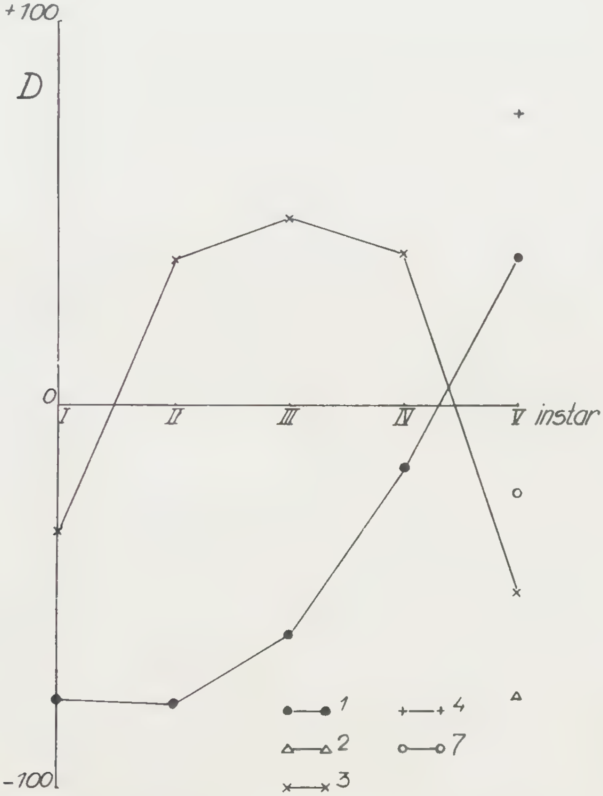

Fig. 3. *Laothoe populi* L. Experiments on the orientation of larvae crawling on bare twigs.
1: thin horizontal twigs, lighted from above; 2: thick horizontal twigs, lighted from above; 3: thin horizontal twigs, lighted from below; 4: thick horizontal twigs, lighted from below; 7: vertical twigs, lighted from one side.

The following experiment, made on two full-grown Eyed Hawk larvae, crawling on thick horizontal twigs lighted from above, shows that the eyes are the sense organs responsible for the light reaction. We first observed the behaviour of the intact larvae in the usual way. We then covered their ocelli with black cellulose paint, and repeated the observation. The results were as follows:

	dd	*vv*	*oo*	*D*
ocelli open	1	26	4	+ 81
ocelli covered . . .	44	0	0	—100

Though in view of the findings of WATERHOUSE (1953) we must be very cautious in the interpretation of experiments of this sort, I think it can be concluded that the eyes are the sense organs for the light reaction if we also take into account the fact that the normal light reaction returned when we removed the paint from the ocelli, and that painting of other small areas of the body did not affect the behaviour of the caterpillars. The negative value of *D* when the ocelli were covered must be due to the unhampered expression of the negative geotaxis.

In the preceding pages we have only considered the mutual comparison of countershaded species belonging to different taxonomic units, but obviously the comparison of one such species with non-countershaded relatives will be equally interesting. The closer in the latter case the relationship is, the more revealing we may expect the comparison to be. Therefore, a few words may now be said about the larvae of the Poplar Hawk, *Laothoe populi* L., a very close relative of the Eyed Hawk.

The pattern of *populi* consists of the same elements, and has the same anatomical basis as that of *ocellata*. However, the pigmentation gradient is so slight that the *populi* larva must be called non-countershaded, and the dark edges along the slanting stripes are poorly developed.

Even when full grown, *populi* larvae always sit on the underside of the leaves of their food plants. Our data on the behaviour of crawling *populi* caterpillars are summarized in fig. 3. This shows that in the first instars their orientation is similar to that of *ocellata*. However, in the fifth instar the *populi* larva still prefers dorsal light on a vertical twig (fig. 3, graph 7), though on a horizontal thick twig light seems to have no influence (graphs 2 and 4). In any case, there is no negative phototaxis. Geotaxis is markedly negative in all instars.

2. *Mimas tiliae* L. (Sphingidae). This species is also rather closely related to *ocellata*, and its larva is essentially similar in pattern to the Eyed Hawk caterpillar. There are no differences that we need discuss here between the two species as regards the anatomy and ontogeny of their patterns, apart from the fact that in the Lime Hawk the pigmentation gradient is less steep. There is, however, an interesting difference in behaviour between *ocellata* and *tiliae*. Even when full grown, *tiliae* larvae always sit on the underside of the lime leaves, and not on the twigs.

In one experiment with two freshly caught full grown specimens of *tiliae* I found no orientation whatsoever to light in the larvae when crawling on a vertical bare lime twig, lighted from one side by a 100 W bulb at a distance of 80 cm. However, when crawling onto a leaf the larvae in all cases selected its shadow side. If this was the underside of the leaf, they crawled on at once. If, however, the upper side was turned away from the light, the caterpillar made numerous searching movements on this side, but did not crawl onto the leaf. It appeared that the larvae were quite unable to hold on to the smooth upper side. However, they never crawled onto the lighted underside in these circumstances.

In 1952, our *tiliae* culture unfortunately was wiped out by disease. All I can conclude from our observations in that year is that the behaviour of the first instar of the Lime Hawk is entirely similar to that of *ocellata* or *populi* (see Table 1).

3. *Sphinx ligustri* L. (Sphingidae). The pattern of the full grown Privet Hawk caterpillar is rather more difficult to interpret than are those of *ocellata* and *tiliae*, but in any case the large caterpillars have good inverted countershading. There are no subdorsals, but the usual seven pairs of slanting stripes are present. The latter are pure white, edged dorsally with a dark purple band of about the same width as the white. The ventral boundary of the white, and the dorsal edge of the purple are quite sharp. Consequently the illusion of prominent ridges is less perfect in this species. Of course, the pattern has a certain disruptive effect, but this is lessened by the fact that they are shorter than in *ocellata*. In addition, the head and the horn on the last segment have bold black markings in *ligustri*, whereas in *ocellata* and *tiliae* both are inconspicuously coloured. Apart from its countershading and ground colour, the pattern of the Privet Hawk larva is therefore somewhat reminiscent of (pseud)-aposematic rather than cryptic coloration. In this context it should be mentioned that the behaviour of our Jays sometimes suggested that they found *ligustri* less palatable than *ocellata* or *tiliae*. We have not made systematic tests to prove this point.

All this cannot detract from the fact that the Privet Hawk caterpillar has excellent inverted countershading. Practically the whole pattern is located in the hypodermis. Its development is quite gradual. Yellow subdorsals are present at first, but disappear in the third instar. The oblique stripes are present from the first instar onwards, but are yellow at first. Countershading begins to appear in the second instar, but the gradient does not attain its final steepness until the fourth, when also the slanting stripes have become white and have acquired their purple edges.

There are considerable irregularities in the results of our experiments on the orientation of crawling *ligustri* larvae (summarized in fig. 4), but they form a sufficient basis at least for the following conclusions. The leaved twigs of privet are very thin. On thin horizontal twigs, lighted from above, *D* gradually changes from negative to strongly positive in the course of the successive instars, so that in the fifth pattern and behaviour are in perfect harmony. This is in agreement with field

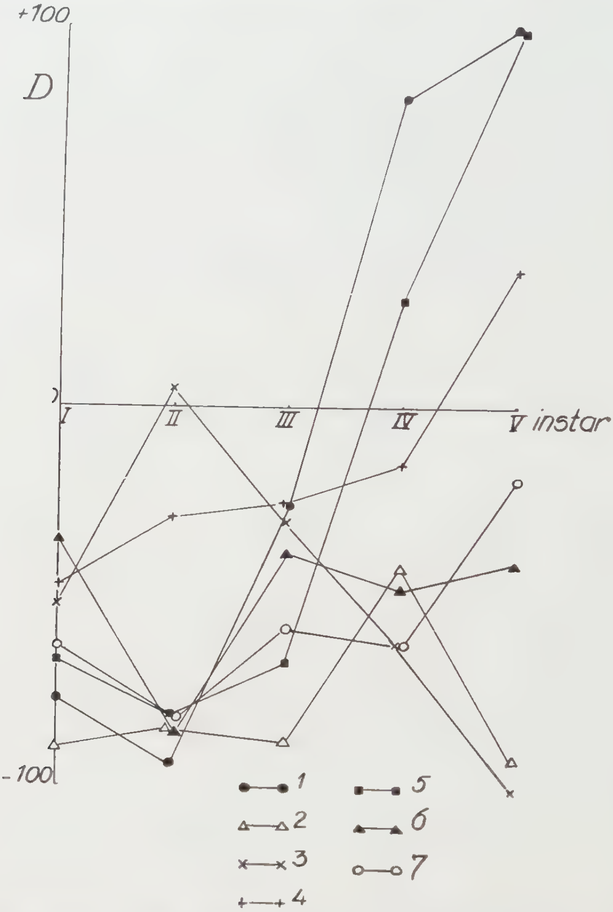

Fig. 4. *Sphinx ligustri* L. Experiments on the orientation of larvae crawling on bare twigs.

1: thin horizontal twigs, lighted from above; 2: thick horizontal twigs, lighted from above; 3: thin horizontal twigs, lighted from below; 4: thick horizontal twigs, lighted from below; 5: thin horizontal twigs in diffuse light; 6: thick horizontal twigs in diffuse light; 7: vertical twigs, lighted from one side.

observations: in the wild, full grown *ligustri* caterpillars always turn their dark belly to the light.

In our experiments the transition from negative to positive *D* under "normal" circumstances (fig. 4, graph 1) took place between the third and fourth instars. In other words, as in *ocellata*, it coincides with the migration from leaf to twig. The younger instars of *ligustri* always sit on the underside of the leaves. Casual observation is enough to make it clear that, in fact, the midrib of this side of the leaf is the only part of the plant which offers them sufficient foothold. It may be noted that, especially in the first instar, the larvae are deceptively similar to this midrib. It is not until the fourth instar that the caterpillars become too big to find adequate shelter on the underside of the leaves, and move to the twigs:

number of larvae on	Instar I	II	III	IV	V
leaf . . .	45	44	52	8	0
twig[1] . . .	6	10	12	16	50

As regards the cause of the change in *D*, the data compiled in fig. 4 show that this is not due to a change in phototaxis or geotaxis, but merely to passive obedience to gravity in the later instars. On horizontal thick twigs in diffuse light (fig. 4, graph 6), the upper side is always preferred. On vertical twigs lighted from one side (fig. 4, graph 7) *D* is negative in all instars, *i.e.*, there is a preference for dorsal light. There is some suggestion that this may decrease in the later instars. On thin horizontal twigs in diffuse light (graph 5), *D* changes in approximately the same way as on thin horizontal twigs lighted from above (graph 1). This is a further argument that no negative phototaxis plays a role in the adaptiveness of the behaviour of the full grown larva. As the set up of our experiments with diffuse light was not very satisfactory, no further conclusions should be drawn from the differences between graphs 1 and 5 in fig. 4.

4. *Macroglossum stellatarum* L. (Sphingidae). The larvae of the Humming Bird Hawk Moth are dimorphic. Of the two forms, one dark brown and one green, I have reared only the latter, and the following description refers to that form. To my surprise some brown specimens which I obtained in England showed no countershading. It would be worth while to investigate whether this is correlated with a similar difference

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[1] These data were obtained in experiments on leaved twigs in the laboratory; probably the percentage of larvae on the twig in the younger instars is somewhat too high, owing to mutual disturbance.

in behaviour between the brown and green forms as was described by Sevastopulo (1945) for another group of Sphingid caterpillars, *viz.* the Chaerocampids.

By comparison with the foregoing species, *stellatarum* larvae are quite small. They hardly exceed in length the leaves of the larger species of the Rubiaceous family on which they feed, and whose colour they match closely. It is characteristic of this group of plants that their leaves are folded along the midrib, and have no conspicuous lateral veins. The pattern of the larva is a striking adaptation to this environment. It has double inverted countershading, but, when full grown, no other markings whatsoever . The ground colour is darkest at the ventral side. From there, it gradually lightens so that it merges almost imperceptibly into the white subdorsal which extends over the whole body. Dorsally, the subdorsal is set off by very dark green, which in its turn grades into a much lighter colour on the mid back. The result is that, to the human eye, the body wall under normal lighting conditions does not look cylindrical, but seems to consist of two flat planes which intersect in the subdorsal, just as the leaf consists of two flat halves that meet in the midrib. Following Süffert, we shall use the term "contrast line" for the boundary between the two countershaded fields in patterns of this type.

Dissection of a single specimen gave the following data on the localisation of the pattern. The hypodermis contains the white subdorsals. Dorsally to these, it is light green, without gradation, and so opaque that it completely screens off the white fat body. In the midventral region, the hypodermis is practically colourless and transparent. However, it becomes more opaque and whiter towards the subdorsals. In the dorsal region, the cuticle has a green pigmentation, light in the middle, but darkening towards the subdorsals. At the latter, this pigmentation ends with a sharp boundary. All more ventral parts of the cuticle are only very slightly grey, except in the areas overlying the subdorsals and laterals *(v.i.)* where it has no pigment at all. Blood and gut both are green. Their removal has little or no influence on the appearance of the parts dorsal to the subdorsal, but, in marked contrast, it leaves the lateral and ventral regions pale yellow. Evidently the countershading depends on different factors in different parts of the body, *viz.* on the superpositon of a shaded cuticle on a plain green hypodermis in the dorsal field, and on belly and sides on the increased screening off of blood and gut by the the hypodermis toward the subdorsals.

The pattern of the Humming Bird Hawk larva develops gradually. Countershading becomes visible later than in any of the previous species, *viz.* not till the third instar, and even then it is still very weak.

In the first instar, a pair of white laterals appear, which persist until well into the fifth instar. In the third instar these have turned a bright yellow, and are more conspicuous than the subdorsals. After the next moult they are somewhat faded, but they remain a disturbing factor, reducing the effectiveness of the countershaded pattern. It is only in the course of the last instar that they disappear completely.

In my culture, feeding and resting caterpillars usually sat belly upwards, as required by their countershading. A small set of observations on the behaviour of crawling *stellatarum* larvae, made under circumstances that differed from our standard conditions in 1952, suggest that the larvae have a strong preference for dorsal light. Moreover, as might be expected in view of their small size, they have little difficulty in maintaining themselves on very thin twigs. Therefore, I suspect that the structure of the leaves will play an important role in bringing the larvae into the normal position.

5. *Cerura vinula* L. (Notodontidae; plate II). The larva of the Puss Moth is famed for its surprising number of adaptations against predators. When full grown, it is concealed by colour resemblance with its environment, double inverted countershading, disruptive patterning, and disguise of its outline by its unusual shape and attitude. If, in spite of all this, it is attacked, it tries to ward off the enemy (1) by displaying two conspicuously coloured "tails", normally hidden in the modified stemapods, and (2), more effectively, by jerking towards the attacker its fore part with the red "collar" on the first segment made conspicuous by the retraction of the head, and squirting in his direction a jet of 40% formic acid (POULTON, 1890). In addition, the younger instars have a cryptic pattern of an entirely different nature. Of all these features, we shall here discuss only those that are relevant to the problem of countershading.

The contrast line is formed here by the white band separating the more or less brownish, strangely shaped disruptive saddle patch on the back from the green sides. Our observations on the ontogeny of the pattern show that this band is not homologous with the subdorsals. The green ground colour is darkest ventrally, and becomes gradually lighter toward the white band. In the dorsal patch, countershading is due to a fine irregular pattern of tortuous white lines, forming a network the meshes of which are wider laterally than on the mid back. As we shall presently see, the full grown larva usually sits on the underside of the twig. In this position it seems to consist, owing to its pattern, of two flat planes, one green and one brownish, which intersect in the white band.

The green colour is entirely due to the pigments of the blood.

Removal of the blood leaves all green parts of the body pale yellow, but still countershaded. It does not affect the dorsal patch, which, together with the white band, is located in the hypodermis. Ventrally and laterally, the hypodermis is yellow. This yellow is graded. Near the white band it is very pale, and here the hypodermis is thick and opaque. More ventrally, the yellow becomes darker and the hypodermis more transparent and thinner. The cuticle is almost entirely colourless, being only slightly bluish when viewed against a dark background. Evidently, countershading in the Puss Moth caterpillar is due to the hypodermis alone.

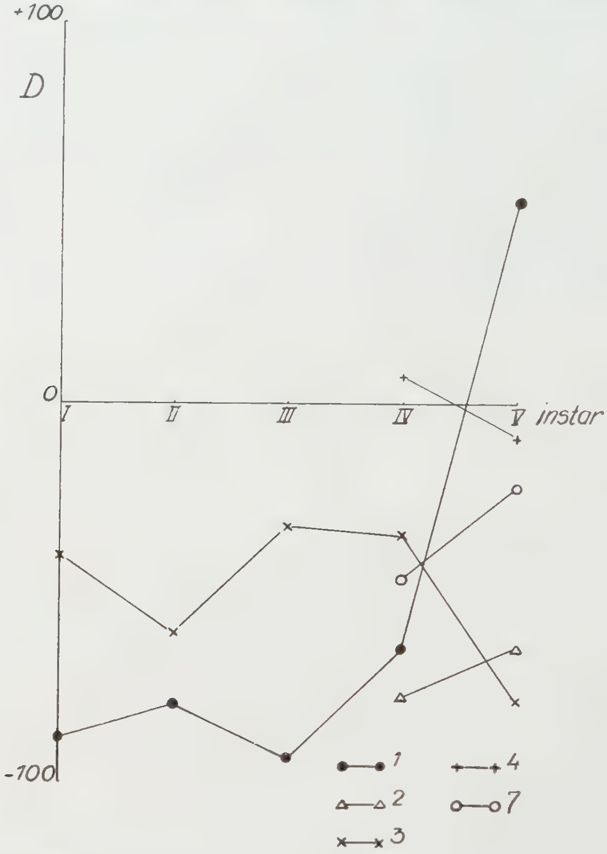

Fig. 5. *Cerura vinula* L. Experiments on the orientation of larvae crawling on bare twigs.
1: thin horizontal twigs, lighted from above; 2: thick horizontal twigs, lighted from above; 3: thin horizontal twigs, lighted from below; 4: thick horizontal twigs, lighted from below; 7: vertical twigs, lighted from one side.

In *vinula*, countershading develops even later than in *stellatarum*. In the dorsal patch it can first be seen in the third instar, but in the lateral field it does not appear till the fifth. The first four instars of the Puss Moth larvae sit on the upper side of poplar and willow leaves, on a small mat spun of silk. Only in the fifth instar, when the main increase in their size takes place, they are habitually found hanging on the underside of twigs and leaf stalks.

As fig. 5 shows, only passive obedience to gravity, of the factors investigated, is responsible for bringing the larvae into the adaptive position. They always retain a preference for the upper side of the twig and for dorsal light, but in the end these preferences are overruled by the pull of gravity which on their natural food plants the larvae cannot resist. It is interesting that *D* under normal circumstances becomes positive only in the last instar. This fits in well with the very late development of countershading.

6. *Notodonta ziczac L.* (Notodontidae). A very good description of the full grown larva of this species was given by SÜFFERT (1932), who pointed out that it is effectively concealed by (1) disguise of the outline by a combination of strange shape and unusual resting attitude, and (2) by double inverted countershading. The contrast line is formed here by a suprastigmatal lateral stripe. In addition to those mentioned by SÜFFERT, the larva possesses a very different means of protection: it can produce a drop of acid to deter an attacker, though it will do so much less readily than the Puss Moth caterpillar. The development of the pattern is quite gradual. Countershading appears in the second instar.

SÜFFERT found no reaction to light in the feeding and resting caterpillars, and assumed that a reaction to gravity brings it into the adaptive attitude. Our observations on the behaviour of crawling *ziczac* larvae give some support to this conclusion (Table 1). However, they suggest that the "reaction" to gravity is mere passive obedience. A more complete analysis will be necessary.

7. *Peridea anceps* Goeze (Notodontidae). I have no personal experience of this species which is reported to be one of the best examples of single inverted countershading. Dr. TH. ALBERDA has kindly put at my disposal the following data. In their natural environment, *anceps* larvae always seem to turn their dark side to the light when feeding and resting. The position of the larvae can be influenced by changing the position of the light source. However, the caterpillars do not always adjust their body as a whole to the direction of the light, but often only thorax and head. In lateral light, these parts are then bent and twisted so that they turn their dark ventral side to the light. In dorsal light, thorax and head are sometimes even bent back over the abdomen so that the head is held over the anal segment.

8. *Stauropus fagi* L. (Notodontidae; plate 1, 2). The weird apparel of the fullgrown Lobster caterpillar has baffled all attempts at interpretation (HAACKE, 1893; MÜLLER, 1879; POULTON, 1888, 1890). For its general appearance, it has been likened to a Crustacean, but also to a bunch of dry leaf-bud scales of the beech trees on which it feeds. Its defensive behaviour has reminded probably all observers since ALDROVANDUS of a spider. The end of its abdomen, with the strange stemapods, has been compared to a bug; certain black marks on its body have been interpreted, by no less an authority than POULTON, as false sting-marks of parasites which would deter these enemies from ovipositing in the larva by suggesting that the host is already occupied. In addition, the full grown larva has a well developed acid gland, and, finally, the younger instars have a very pronounced similarity to large ants, both in shape and in behaviour. Some items in this list undoubtedly are the product of phantasy, and nothing is known about the protective value of the remainder, but this at least is certain that the full grown Lobster caterpillar is quite inconspicuous because of its dull brown colour, its highly unusual shape and its immobility, and that this effect is enhanced by its double inverted countershading.

This countershading is very similar to that of *ziczac*, to which *fagi* is rather closely related, as evidenced also by its resting attitude. In the Lobster, as in *ziczac*, suprastigmatal laterals form the contrast lines. For reasons of space, I must refrain from describing the pictorial relief which very effectively accentuates the strange shape of the body. An account of this aspect of the pattern will be published elsewhere.

On dissection, the hypodermis proves to be rather pale brown, somewhat darker ventrally than dorsally, but with a much less steep gradation than one would expect in view of the marked countershading of the intact larva. The hypodermis also shows the stripes and other markings, but in lesser contrast than in the living larva. The intensification of the pattern is due to the cuticle, which contains the full pattern, countershading included, in a very contrasty pigmentation of blackish brown. The pale green blood has no influence on the appearance of the caterpillars.

The development of the pattern is gradual. Yet the younger instars look very different from the full grown caterpillar, and are, as already said, very similar to ants of the *Formica rufa* type. The analysis of this fascinating resemblance, probably a case of mimicry, must be reserved for another paper. The likeness persists until the third instar. Only in the fourth instar the Lobster caterpillar acquires a dull brown colour. At this stage, it also becomes less active, and countershading appears. From now on, the larvae apparently rely in the first place on camouflage.

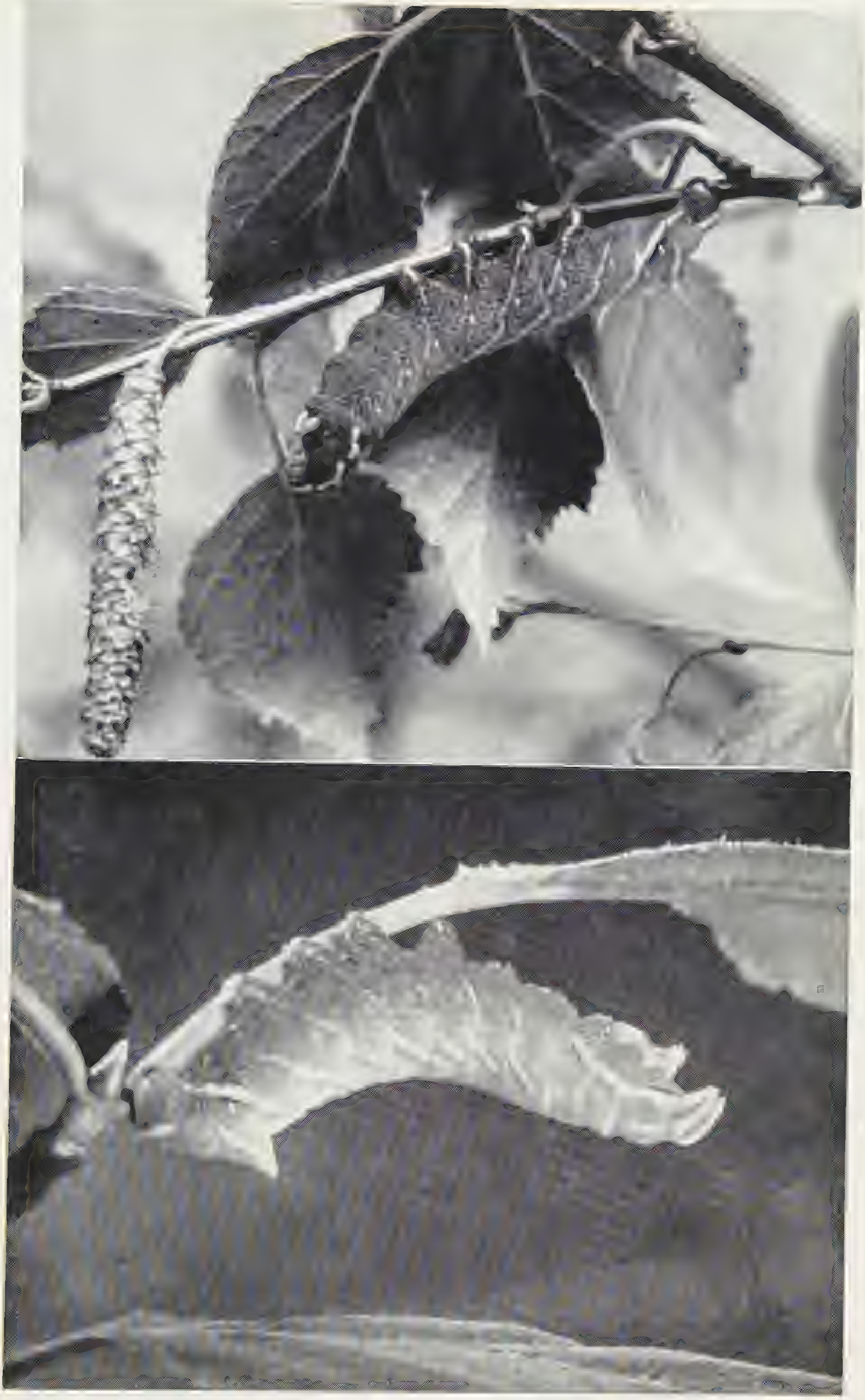

Plate III. *Endromis versicolora* L. Full grown larva photographed under natural circumstances (above), and in diffuse light (below). The latter picture shows the pigmentation gradi

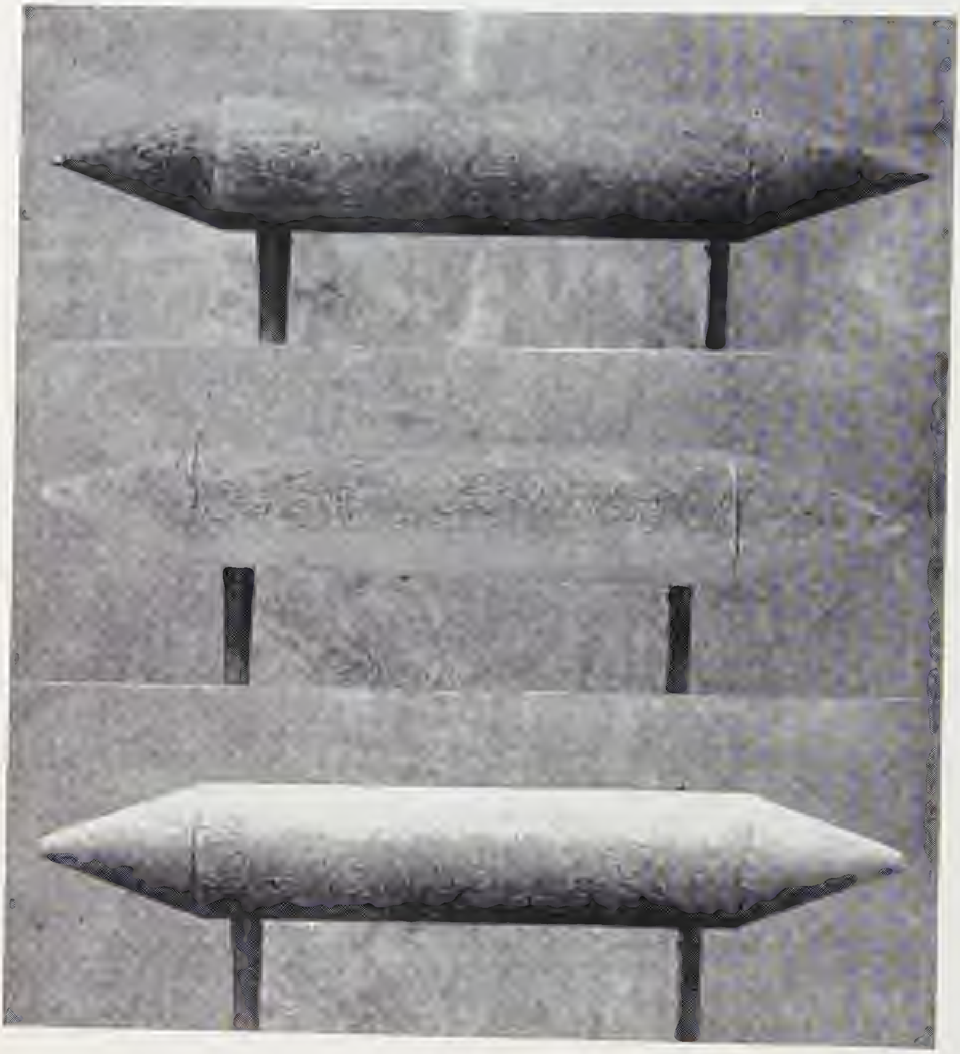

Plate IV. Some of the models used in the discrimination tests. Above: cylindrical model, middle: countershaded model (normal position), below: countershaded model (inverted). The models are seen against the background used in the tests.

My data on the behaviour of crawling Lobster larvae (Table I) indicate a strong preference for the upper side of the twig. In IV, and perhaps also in V, light does not seem to influence their orientation. On our thin twigs, passive obedience to gravity dominates the behaviour of the fifth instar larva. On the thicker twigs of its food plant, however, it can easily maintain itself on the upper side. Yet some observations indicated that the larvae under natural circumstances attain the correct position by passively yielding to gravity.

9. *Lophopteryx capucina* L. (Notodontidae). The countershading of this species is less "good" than that of any of the foregoing. The ventral field, between the two yellow laterals, is plain green. The dorsal half of the larva is bluish green. The midback is almost white. From there, the colour deepens towards the laterals in a somewhat irregular manner, as there are traces of a pattern of alternating dark green and light longitudinal bands. Probably this is a phylogenetically primitive pattern. For that reason, *capucina* is of special interest in connection with the problem of the evolution of countershading. On the thorax there is no countershading at all.

The green colour is due mainly to the blood. The hypodermis is white dorsally, more yellow and less opaque ventrally. It contains the laterals. The cuticle is practically colourless. The exact tone of the ground colour is determined by the hypodermis with its varying content of yellow pigment. Countershading is due to the dorsally increased screening effect of the hypodermis.

Even as late as the fourth instar, the larvae are not yet really countershaded but wear a pattern of longitudinal yellow subdorsals and laterals on a green ground colour. However, the subdorsals have already expanded greatly into the dorsal field, and the lateral field has assumed a yellowish tinge.

10. *Colias croceus* Fourcroy (Pieridae). SÜFFERT has chosen the caterpillar of the Clouded Yellow as the "paradigmatischer Einzelfall" with which he opens the presentation of his data. Nothing needs to be added to his elaborate description of the full grown larva. It differs from all species so far discussed here in that its double countershading is not inverted. The green ground colour is darkest on the mid-back, and from there it gradually lightens until the light laterals are reached. At the ventral boundary of the latter, the green at first is very dark again, but lightens towards the median line of the belly and the tips of the prolegs.

My findings on the anatomy of the larva agree completely with SÜFFERT's results. The green ground colour and the laterals are localized in the hypodermis. Countershading is due to the co-operation of hypodermis and cuticle. The latter has a graded pigmentation of melanin, whereas the hypodermis itself is graded both as regards its opacity and the intensity of its green pigmentation. The development of the pattern is gradual. The green colour is present from the second instar. Laterals and countershading appear in the third.

Süffert states that larvae in the first four instars are always found on the upper side of the leaves of their food plant. Full grown larvae often sit on stems or leaf stalks, always turning their backs to the light, even if, in experimental conditions, this comes from an unusual angle. Süffert has not found any influence of gravity on the orientation of the larvae, but he made no quantitative experiments to determine whether such influence is in fact completely absent. The main method by which the larvae attain their normal position is to crawl in a spiral around the stem, until they have reached the desired orientation. Apart from this, the tilting reaction which we shall discuss in the next species, has also been found in *croceus*, but here it is slow and its amplitude is small. Crawling *croceus* larvae have a strong preference for dorsal light.

A final point of great interest is that Süffert found that the pupae of *croceus*, which, as all girdle pupae, hang with their ventral side upwards, have inverted double countershading.

11. *Gonepteryx rhamni* L. (Pieridae). The caterpillar of the Brimstone is similar to that of the Clouded Yellow. My observations on this species completely confirm Süffert's description. The ground colour of the full grown *rhamni* larva is darkest on the midback. From there it gradually lightens toward the white laterals, into which it melts imperceptibly. The ventral field is also countershaded.

Practically the whole pattern is located in the hypodermis, though in the latter's more transparent parts blood and gut may also play a role. The exact shade of the ground colour is determined partly by the even grey pigmentation of the cuticle. The development of the pattern is gradual. Countershading is clearly visible from the third stage onwards.

First instar larvae of *rhamni* are to be found on both sides of the buckthorn *(Rhamnus catarctica)* leaves. All later instars, however, sit only on the upper side of the leaves. The larvae have a strong preference for dorsal light. When on a twig, they crawl in a spiral until they have attained the correct position. On the flat leaves, however, this sort of adjustment is impracticable. It is highly significant that, as Süffert found, the larvae here use a different means to achieve the same result. When lighted from one side, the larva tilts its body by contracting the legs on that side, and stretching those of the other side. This reaction is very rapid, and has a surprisingly wide amplitude (more than 90° each way). SÜFFERT has shown that in this case the light stimulus is perceived not by the eyes, but by a diffuse sense in the skin of the whole body.

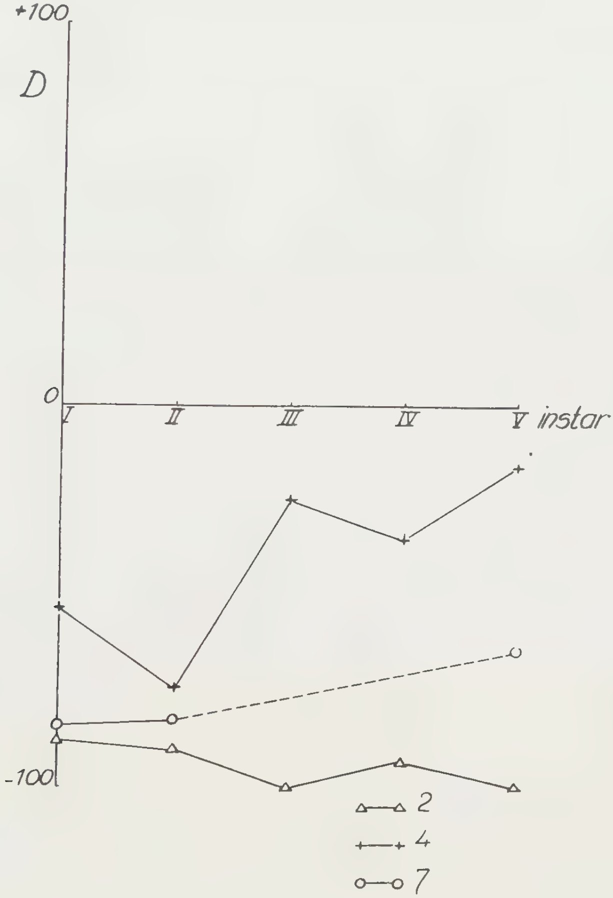

Fig. 6. *Endromis versicolora* L. Experiments on the orientation of larvae crawling on a bare twig.
2: thick horizontal twigs, lighted from above; 4: thick horizontal twigs, lighted from below; 7: vertical twigs, lighted from one side.

The pupa of the Brimstone shows adaptive coloration of a type similar to that of *croceus*.

12. *Endromis versicolora* L. (Endromidae; plate III). Interesting problems are raised by the development of the caterpillars of the Kentish Glory

(De Ruiter, 1954). They begin life with an aposematic pattern and gregarious habits. Gradually, however, they develop a beautiful camouflage, and become solitary. However, in this species, the cryptic habits develop rather later than the concealing pattern. When full grown, the larvae have a green ground colour with strong inverted countershading, and a pattern of slanting white stripes, edged with darker green especially on the dorsal side. It is interesting that the latter, in spite of their similar appearance, are probably not homologous to those of *tiliae* and *ocellata*, as in *versicolora* they slant down backwards, instead of forwards as in the Sphingids.

The green ground colour is due to the interaction of the blue green blood and the yellowish hypodermis. The latter is responsible for the exact adjustment of the ground colour to the shade of the leaves. In addition, it is the seat of countershading, being white and opaque dorsally, but becoming gradually more yellow and translucent towards the ventral side. The hypodermis also contains the slanting stripes. The cuticle is light grey, marked with many small black dots. The latter are larger, darker and more numerous ventrally than dorsally, and thereby support the countershading.

In nature, feeding and resting *versicolora* larvae are always found hanging on the underside of twigs and leaf stalks. When crawling, they very clearly prefer the upper side of horizontal twigs. On thin twigs, however, their weight will often pull them down to the underside. This will happen especially to feeding larvae, which are supported only or mainly by the flexible leaf stalk. It should be added that the larvae crawl very seldom, and if they do, only for short distances. They never move when alarmed by vibrations of the twig. Our experiments (fig. 6) on crawling *versicolora* larvae confirmed that the caterpillars have a preference for dorsal light and for the upper side of the twig until they pupate.

Experiments in which, in a dark room, different parts of the body of a *versicolora* caterpillar were exposed to a very narrow beam of light showed that the eyes are the sense organs responsible for the light reaction.

13. *Charaxes jasius* L. (Nymphalidae). This mediterranean species, on which Süffert made some observations, always sits on the upper side of the leaves of its food plant, where it remains motionless as long as there is daylight. It is green, with inverted double countershading, the substigmatal lateral acting as contrast line. Countershading is located in hypodermis and cuticle. There is a very strong tilting reaction in this species.

14. *Apatura ilia* Schiff (Nymphalidae). This species, according to Süffert, combines longitudinal and normal countershading. This remarkable pattern is in good agreement with its normal position, sitting vertically on the upper side of hanging

leaves. It reaches this position by means of reactions to light (direction and intensity), gravity, and the structure of the plant. Once the caterpillar has attained its resting position, its only further reaction is a strong tilting, which ensures that the larva always has dorsal light. Experiments on the localisation of the receptors led to the same result as in *rhamni*. The pupa which hangs head downwards, instead of upwards as the caterpillar, also has longitudinal countershading, but in harmony with its position the direction of the gradient is here opposite to what SÜFFERT found in the larva.

15. *Papilio podalirius* L. (Papilionidae). SÜFFERT states that this species, just as *ilia*, combines normal and longitudinal countershading. It also has the same resting position. Here, as in *ilia*, reactions to both light and gravity were found. However, the influence of gravity is far weaker than in *ilia*. It is interesting that *podalirius*, though its countershading is not double, has a lateral.

16. *Actias selene* Hb. (Saturniidae). SÜFFERT described larvae of this species. When full grown, they have double inverted countershading, the substigmatal lateral acting as contrast line. They normally hang on the underside of the twigs of their food plants. This is due to light and gravity reactions. The first reaction of the larva to lateral light is tilting, but as a rule this is followed sooner or later by locomotion which brings the animal into the correct position. In addition, the same bending and twisting which ALBERDA found in *Peridea anceps* can be observed in *selene*.

SÜFFERT's description of the localisation of the pattern is not entirely clear. The cuticle has marked single countershading. The double countershading of the entire pattern must be due to the hypodermis, which also contains the contrast line and part of its pictorial relief. Another part of the latter, however, is due to the cuticle.

17. *Rothschildia orizaba* Westw. (Saturniidae). According to SÜFFERT the "Zweiflächeneffekt" of double countershading is most complete in this species. Yet, judging by his description of the localisation of the pattern, the ventral field is not countershaded. The parts dorsal to the substigmatal lateral which acts as contrast line are beautifully countershaded. This gradation is due to the hypodermis alone. The larva adjusts its position by tilting, bending and locomotion.

D. DISCUSSION

We must now summarize these data in order to see to what conclusions they lead. The above list of countershaded species is anything but complete. Its composition was determined solely by the availability of material. Yet it illustrates to some extent the fact that the occurrence of countershading bears no relation to taxonomic divisions. Graded pigmentation occurs in widely different families, but it may be absent in the nearest relatives of countershaded species (*e.g.*, *ocellata* and *populi*).

On the other hand, there is some connection between the occurrence of countershading and the ecological properties of caterpillars. All countershaded larvae so far described have cryptic patterns. Hence, in view of the strong positive correlation (COTT, 1940) between inconspicuousness and palatability, they may be expected to be relatively palatable. What little evidence we have (chapter III; STEINIGER, 1938) certainly confirms this expectation. In such species as *fagi* and *versicolora*, countershading appears only when the conspicuous elements of pattern and behaviour have disappeared.

Anatomically, the patterns of different countershaded species often are extremely unlike. Even the direction of the gradient can vary (Table II). Moreover, there can be either one uninterrupted gradient over the whole body, or two gradients. In the latter case, the contrast line (p. 306) may be either the subdorsal, or the lateral, or yet another element. Little is known of the homology of pattern elements in caterpillars, but it may be important to distinguish between substigmatal, stigmatal, and suprastigmatal laterals among the contrast lines. Further research on this point, and indeed on the homology of larval patterns in general might prove fruitful.

TABLE II

Single Countershading			
	Ventrodorsal gradient:		*ocellata*
			tiliae
			ligustri
			anceps
			versicolora
	Dorsoventral gradient:		*ilia*
			podalirius
	Rostrocaudal gradient:		*ilia*
			podalirius
Double Countershading			
	Ventrodorsal gradient:		
		Subdorsal contrast line:	*stellatarum*
		Substigmatal lateral contrast line:	*selene*
			orizaba
		Suprastigmatal lateral contrast line:	*ziczac*
			fagi
		Other contrast lines:	*vinula*
	Dorsoventral gradient		
		Stigmatal contrast line:	*croceus*
			rhamni
		Substigmatal contrast line:	*jasius*

The seat of the gradients also varies among species. Table III gives

TABLE III

hypodermis	hypodermis and blood	hypodermis and cuticle	hypodermis, cuticle and blood
ocellata	*vinula*	*fagi*	*stellatarum*
tiliae	*capucina*	*croceus*	*versicolora*
ligustri		*jasius*	
rhamni		*ziczac*	
		selene	

a somewhat schematic summary of the available data on this point. In this table, only the main contribuents to the patterns are mentioned, and it should be realised that there may be considerable differences in the mode of action of each organ among the species listed in the same column.

What little data we have on the evolution of graded pigmentation suggests that here, too, differences will occur. In *capucina*, countershading has apparently developed by a process of expansion and blurring of longitudinal stripes. In the Sphingids, countershading probably has another origin, for here the subdorsal *(ocellata, ligustri)* and the lateral *(stellatarum)* may still be sharply defined at a stage when the ontogeny of countershading is almost completed.

There is one morphological property, however, which all countershaded caterpillars have in common. The pigmentation gradients on different parts of the body are always so directed that in the animal's normal resting attitude they are parallel to one another. Perhaps the most striking examples of this principle are provided by species with such bizarre resting attitudes as *fagi*, but others can be found in all cases of double countershading and pictorial relief.

A similar harmony, but between less closely related characters, and therefore of greater interest, transpires from the comparison of behaviour and pattern of countershaded caterpillars. In this context, the parallel should be mentioned between, on the one hand, the patterns of *stellatarum* and, *e.g.*, *ocellata*, and on the other hand the appearance of the leaves among which they live. Both types of pattern are common in the Sphingid family (Mell, 1922; Moss, 1920; Rothschild and Jordan, 1903; Weismann, 1876), and it would be interesting to see whether the same correlation between pattern and type of food plant selected will be found in all cases.

Still more important is the fact that without an exception all countershaded caterpillars turn their darkest side to the light in their natural environment. How closely pattern and behaviour are linked can be seen especially from the ontogeny of these larvae: the graded patterns and the concomitant behaviour as a rule develop at very nearly the same time. The only exception to this rule I know is *versicolora* (De Ruiter, 1954). This species differs from all others in that its larvae initially are gregarious. Apparently the advantages of this habit, which may cause an acceleration of development (as demonstrated in *Vanessa* by Mosebach, 1938) outweigh that conferred by countershading until a fairly late stage in development. Another striking instance of the parallel between pattern and habits is formed by such cases as *croceus* and *rhamni*, where a reversal of gradients coincides with the change in habits involved in pupation.

The significance of these parallels is enhanced by the fact that on analysis the underlying behavioural mechanisms are found to be as varied as the morphological constituents of the patterns.

All Lepidopterous larvae so far investigated are negatively geotactic, and the great majority of them, as well as of other insects, prefer mid-dorsal illumination ("Lichtrückenreflex", BUDDENBROCK, 1952; dorsal light reaction, FRAENKEL and GUNN, 1940). Therefore, it is of no special interest if, as in species with normal countershading, we find that these reactions guide the caterpillars into the right position. A very remarkable group, however, is formed by species with inverted countershading. Some of these, indeed, have retained their preference for dorsal light *(ligustri, versicolora, stellatarum, vinula)*, but in others we find a reversed light reaction *(ocellata, selene)*, and probably a few others *(fagi*, and perhaps *ziczac)* which do not yet prefer ventral light, at least have no predilection for dorsal light either. To my knowledge, a ventral light reaction is not found in any non-countershaded species. Even in *populi*, which is very closely related to *ocellata*, we find the normal dorsal light reaction. We do not know why only some of the species with inverted countershading have this adaptive type of light reaction. Perhaps this may be connected with variations in the adaptive value of countershading among species, due, *e.g.*, to the possession of other means of defence or to differences in predation pressure.

Even within the group whose orientation is due to a reaction to light, there are considerable differences both on the receptor and on the effector side in the mechanisms involved. Light may be perceived either by a diffuse sense in the skin, or by the ocelli. The hypothesis might seem tempting that the more primitive reaction (dorsal light reaction) is mediated by the more primitive sense organ (skin). However, this is not tenable. In a number of species with preference for dorsal light, the eyes are the responsible organs *(versicolora, Celerio euphorbiae* L., (DE RUITER, unpublished observations)). As far as I know, the only case of ventral light reaction where this problem has been investigated is *ocellata*, where the ocelli proved to be responsible. On the motor side, the reaction to light may take the form of locomotion, tilting or twisting. It is important that, for instance, tilting, an important element in the behaviour of some countershaded species, has not yet been found in non-graded larvae.

In my opinion, the facts here presented are sufficient to substantiate the statements made at the beginning of this chapter. We must next consider whether they can form a basis for the conclusion that countershading is an adaptation. SÜFFERT has published his data without discussing their interpretation, though in some places he points out what explanation they suggest. In his concluding pages, he makes some remarks on the lines of reasoning to be followed in evaluating such data, but states explicitly that he wants to reserve their full application for a later paper. To my knowledge, this paper was never written.

For that reason we shall discuss the steps involved in our conclusion in some detail. We must first define the term adaptation as used in this paper. An adaptation is any character of an organism that satisfies the following criteria: (1) in its present state, the character must have a greater survival value than it had in the form in which it occurred in the immediately ancestral type living in the same environment, and (2) the increase in survival value must have been one of the causes (either in a Lamarckian or in a Darwinian sense) of its evolution into the present form.

The conclusion that countershading is an adaptation in this sense may be drawn from the indirect evidence given above only if it can be shown that no alternative hypothesis is equally or more probable. It is true that the case could be strengthened very much by taking into account other groups such as Vertebrates and Molluscs (Cott, 1940; Holmes, 1940; Longley, 1917, 1926; Mertens, 1943; Mottram, 1915), but this would lie outside the scope of the present paper.

The following hypotheses must be considered:

(1) that countershading is an entirely conservative character in which no evolution has taken place at all,

(2) that countershading is the result of an evolutionary process that was not influenced by the survival value of the pattern, which may or may not be positive.

(1). Apart even from its improbability, the assumption that countershading is an entirely conservative character can be refuted at once. If this were correct, all graded patterns would have to be morphologically identical. As we have seen, this is certainly not the case. It is even impossible, on the following grounds, to regard all countershaded patterns as homologous derivatives of a common ancestral graded pigmentation.

(a). The direction of the gradient relative to the body axes varies among species. However, all graded pigmentation has the same orientation with regard to the environment: the darker parts are always turned to the light. Therefore, the gradients might be of common phylogenetic origin, being due to the same physiological reactivity to an environmental stimulus in all species. For Vertebrates, this assumption has in fact been made, and the adaptive nature of countershading has been contested on this ground (*e.g.*, Barbour and Phillips, 1911). As pointed out by Hjort (in Murray and Hjort, 1912), the latter conclusion is unfounded, even if countershading would be due to such a mechanism, for the possession of such special reactivity by many species is a strong argument that this reactivity itself must be adaptive. In our caterpillars, however, it is most unlikely that countershading is due to a common mode of reaction to environmental stimuli, as not only the organs carrying the gradient, but even the very pigment itself is not the same in all cases. It would be an even more fatal objection against the hypothesis under discussion if it could be shown that the patterns develop normally in caterpillars reared under abnormal light conditions, *e.g.*, lighted from below. We started an experiment along these lines on *versicolora*, but unfortunately the larvae were killed by disease before countershading could develop.

(b). As already said, our observations on *ocellata* and *capucina* suggest that the evolution of countershading has taken different starting points in these species.

Of course, within restricted groups such as the asemanophorous Sphingids (to which *ocellata*, *tiliae*, and *ligustri* belong), countershaded patterns may be completely homologous. Yet it seems indisputable that countershading is not a conservative character in caterpillars, but that it has arisen independently in many branches of the phylogenetic tree of the Lepidoptera, and that the similarity of the patterns is pure convergence.

(2). The only remaining alternative to the assumption that countershading is an adaptation is the hypothesis that its evolution was not influenced by its survival value. I have argued elsewhere (De Ruiter, 1955 and in prep.) that the evidence available in the case of colour patterns is in good agreement with the almost generally accepted theory (Dobzhansky, 1951; Huxley, 1945; Simpson, 1953; Wright, 1949) that evolution is caused mainly by natural selection from "mendelian populations" (Dobzhansky, 1950). However, as was pointed out especially by Wright (1931, and elsewhere), the course and rate of the selective process will be influenced by chance fluctuations in gene frequencies. The extent of this influence is very insufficiently known. For a complete understanding of any given case, we would need data on the number of genes involved, the number of available alleles of each of these genes, the selective values (and their standard deviations) of all possible combinations of alleles, and the population number. In the case of countershading, we have no data on any one of these points. However, there is one important objection against the hypothesis that countershading is the result of "genetic drift". Drift continually tends to disintegrate any existing gene complex. Hence, it is significant that the variation within species of countershaded patterns is very small. This must be due to the weeding out of aberrant individuals which will inevitably arise, *i.e.*, to the selective advantage of the gene complex resulting in countershading. This implies that this selective advantage must necessarily also have played a role in the spread of this complex over the species, so that the complex satisfies our definition of adaptation.

We must now face the objection that this selective advantage is not due to the graded pigmentation but to some other effect of this gene complex, countershading being an indifferent, or perhaps even slightly detrimental by-product, due to pleiotropy of certain genes of the complex. Two arguments can be advanced against this hypothesis.

(a). The phenotypic expression of a gene is not unalterable. It depends on the total genetic constitution of the organism (FISHER, 1930). A change at other loci may alter the expression of the gene under consideration (FORD, 1940). Therefore, if countershading were a harmful secondary effect of otherwise beneficial genes, we should expect selection to take place for a gene complex in which the injurious effects would be suppressed, without the loss of the favourable effects. There is some evidence that such processes do occur in nature (BLAIR, 1947; FISHER and FORD, 1947). However, if they were taking place in the case of countershading, this would be bound to manifest itself in increased variability of the patterns. Hence, their low variability is an argument that, if a by-product at all, countershading is at least not a harmful one. Now, of course, the probability that any major character of an organism would be completely neutral in its effect on survival value is very small. It is therefore more likely that countershading will have added to the total selective advantage of the genes involved, and will correspondingly have accelerated the evolution of the complex.

(b). On the assumption that graded pigmentation is a mere by-product, the correlation between behaviour and pattern of countershaded caterpillars can be understood only if we assume in addition that the responsible gene complexes also happen to produce the observed behaviour. This is most improbable, firstly in view of the fact that, far from being due to a common reactivity to the environment in all species, countershading almost certainly is caused by different gene complexes in different species, and secondly because the mechanisms underlying the behaviour are widely different. A far more likely alternative is the assumption that all gene complexes which produced countershading in combination with different behaviour have been suppressed by selection. This, of course, means that we regard the combination of graded pigmentation with the "right" behaviour as an adaptation.

At the present stage of our knowledge, very little can be said about the actual course of the evolution of countershading. It is most unlikely that the gene complex as we now find it in a countershaded species will ever have arisen full-fledged by a chance combination. More probably, a preference for a certain orientation with regard to the environment in evenly pigmented species may have been primary. In the absence of any such preference, countershading could hardly have protective value, but a slight preference might be sufficient to give graded pigmentation some selective advantage. With the selection for such a pattern, the selective value of further "improvements" in the behaviour of the caterpillar will have increased. From then on, pattern and behaviour may have evolved hand in hand, until such perfection on both points was reached as we find, *e.g.*, in *ocellata.* The evolution of countershading may therefore have taken much the same course as that of other adaptations in which structure and behaviour of an animal co-operate (Lorenz, 1943; Tinbergen, 1952).

Although the data presented in this chapter seem to form a sufficient basis for the conclusion that countershading is an adaptation, they do not inform us as to the nature of the advantage conferred by graded pigmentation. The only clue we have on this point is the fact that, to the human eye, countershaded caterpillars are less conspicuous than they would be if their pigmentation was not graded. This suggests that the function of these patterns might be to protect the larvae from their natural predators. This conclusion is supported by the observation that graded pigmentation is found only in larvae that are concealingly coloured in other respects as well.

However cogent this conclusion may seem to those who have field experience of the effect of countershading on the conspicuousness of animals to man, it must be realised that it rests on the unproven assumption that the predators' perception is similar to ours. Further evidence is therefore required before we can without reserve accept this hypothesis on the function of countershading.

III. DIRECT EVIDENCE FOR THE PROTECTIVE FUNCTION OF COUNTERSHADING

Observation of the animal concerned in its natural surroundings is the only way to prove that a given character fulfills a certain function. In our case, this means that we must watch encounters between caterpillars and their natural enemies, in order to determine whether the predators are less dangerous to countershaded specimens of a species than to specimens that are non-graded but entirely similar in all other respects.

This raises a practical problem. We do not know a single species with two types of caterpillars, one countershaded and one plain, but similar in all other aspects. This difficulty can be overcome in a way already suggested by STEINIGER (1938). We have seen (p. 293) that countershaded caterpillars are inconspicuous only when in the correct attitude. When inverted, they are very conspicuous. Now the difference between two graded larvae, one inverted and one in the normal attitude, is of entirely the same nature as that between countershaded and non-graded members of the same species, both in the normal attitude. It is true that quantitatively the two cases are unlike, the difference being smaller in the latter: here we are comparing absence of shadow with normal shadow, whereas in the former case we compare absence of shadow with exaggerated shadow. However, if we can show that countershaded caterpillars are in greater danger of predation when inverted than in their normal attitude, the conclusion is unassailable that the countershaded larvae must also be better protected than non-graded members of the same species would be. STEINIGER's attempt to prove the function of countershading in this way remained unsuccessful. As he pointed out, this may have been due to the limitations of his technique. Therefore, we have made a fresh attempt.

We resorted to cage experiments, because it seemed impossible to collect statistically significant data in the field, *e.g.*, by using CARRICK's method (CARRICK, 1936).

As predators, we used Jays (*Garrulus glandarius* L.), not only because this species, an important natural enemy of caterpillars (GOODWIN, 1951), can easily be kept in captivity, but in particular because of its remarkable visual discriminatory powers: a camouflage which protects a species from Jays may be expected with some confidence to be effective against other visual predators as well. A short additional series of tests with Chaffinches (*Fringilla coelebs* L.) was made at Hulshorst.

We have taken every possible precaution to ensure that the encounters between predator and prey took place under practically natural circumstances. All our Jays were hand reared birds that were in good health and not shy of the experimenter. A preliminary series of experiments was made at Hulshorst in 1948 (DE RUITER, 1952b). There we used a cage of 4 × 1 × 1 m, one wall of which was covered with freshly cut twigs of the food plant of the caterpillars used in the experiment. In Wytham we used a much larger aviary, measuring approximately 9 × 9 × 2 m. This was built among shrubbery at the edge of a wood, inhabited by several families of Jays who often visited the neighbourhood of the aviary. It is hardly an exaggeration to say that the aviary was a fenced off part of the natural habitat of Jays. Part of the small trees and shrubs growing in this aviary were birches. These, being the natural food plants of *versicolora* and *tiliae*, we used in our experiments on these caterpillars. For the other tests, we used large bunches of freshly cut branches of willows and privet, placed in jars dug into the soil.

Even the best camouflage can be rendered ineffective by movements of the animal. In our experiments, the inverted larvae, being in an unnatural position were more likely to move than the normal ones. This factor might have falsified our results by adding to the risk of the inverted larvae. We therefore used larvae freshly killed with a small dose of cyanide vapour, and tied to the twigs in a stretched attitude. We found it impossible to imitate the natural resting attitude of the larvae, but it must be remembered that the attitudes of inverted and normal larvae were exactly the same. Due precautions were taken to remove traces of cyanide by airing the larvae before the experiment, and to make the threads with which they were tied invisible.

In all experiments, equal numbers of normal and inverted larvae were used (never more than four of each type per experiment, and often less). We always took scrupulous care to place the caterpillars so that they were equally exposed and equally accessible to the birds. The birds were left without food for some time before the experiment, in order to ensure that they would search actively. In the large aviary we often used two Jays simultaneously, as we found that they hunted independently of each other. We made notes not only of the exact times at which the individual preys were captured, but of the birds' behaviour in general. Each experiment was continued, if possible, until all preys of one type had been found.

We shall see in chapter v that for quantitative purposes the results of such experiments can best be expressed in the form of frequencies of captures of preys of different types. However, the fluctuations in frequency observed in our experiments were so great that the statistical reliability of the conclusions to be reached in this way would not justify the amount of work involved. Hence, we shall content ourselves with a qualitative conclusion, and give the results in a form commonly employed in such investigations (Childs, 1953; Dice, 1947; Ergene, 1951; Popham, 1941, 1943, 1944; for a review of the earlier literature see Cott, 1940), *viz.* the numbers of preys captured (Table iv).

It has been pointed out, *e.g.*, by Dice (1947), that the number of more conspicuous preys will dwindle more rapidly than that of the better concealed ones. Hence, even if we start with equal numbers of the two types, an excess of the latter type will be present in the later stages of an experiment. Now the frequency of captures of preys of a given type will also depend on the numbers present of that type. Therefore, the number of victims among the less conspicuous preys will be relatively too high. In spite of this, as the table shows, in only two out of fourteen

TABLE IV

	number of caterpillars found by							
	Dee		Minstrel		Jean[1]		total for all Jays	
	I	N[2]	I	N	I	N	I	N
versicolora	8	8	3	2	—	—	11	10
tiliae	35	19	11	8	2	0	48	28
ocellata	14	13	14	7	14	6	42	26
vinula	4	4	4	0	26	13	34	17
ligustri	24	23	6	2	2	1	32	26
total for all preys	85	67	38	19	43	19	167	107

[1] Dee and Minstrel were used at Wytham, Jean at Hulshorst.
[2] I = inverted, N = normal attitude.

combinations of one Jay with one caterpillar species, the numbers of normal and inverted larvae captured were equal. In all other twelve cases, more inverted than normal larvae were detected. The opposite was never observed. The numbers of larvae used in our experiments were limited by the availability of material. Consequently, the excess of inverted victims reaches the conventional minimum level of significance ($P = 0.05$) only in the tests with Dee on *tiliae,* though in another case it comes close (Jean-*vinula*).

If for each prey species we add together the tests with all birds, we find an excess of inverted victims in all five, and in two this excess is significant between probability levels of 0.05 and 0.02 *(tiliae* and *vinula)*. On the other hand, if we combine all tests on different preys for each of the birds, we find an excess of inverted victims for all three birds, which is significant at a better level than 0.02 in Minstrel and Jean.

The conclusion seems justified, therefore, that inverted caterpillars run a greater risk from Jays than do larvae in their normal attitude. However, can we assert that this is a consequence of countershading, or could it be due to the mere fact that a caterpillar hanging under a twig is more or less hidden from a bird approaching along that twig? I can offer two arguments to meet this criticism. During the tests in Wytham, we tried to see from which direction the birds detected the caterpillars they captured. Although this was not always possible, we obtained the following data:

		caterpillars captured		
		I	N	total
approached from	below	28	23	51
	same level	6	9	15
	above	7	12	19

This shows in the first place that hunting Jays look upward more often than down, for, among all captures, the excess of larvae detected from below is highly significant. Hence, caterpillars in the normal attitude will be more instead of less exposed, so that the criticism is unfounded in any case. However, our data also show that the proportions of larvae approached from above and below are not significantly different between inverted and normal captured larvae. Therefore, the excess of inverted victims must be due to countershading.

Another check on this point was provided by a series of controls run at Hulshorst, in which we used 12 pairs of *vinula* larvae painted a uniform green so that they were not countershaded, but otherwise unchanged. The quantitative results of such a small series (7 inverted and 9 normal larvae captured) are of little importance, but we made some interesting qualitative observations. In the rather small cage used at Hulshorst, we could watch the birds closely. In tests with unpainted larvae, we had noticed a striking difference in their behaviour towards normal and inverted preys. Inverted preys were as a rule seen from a considerable distance, and even if they were detected from nearby, the eagerness with which the Jay jumped at the caterpillar was remarkable. On the other hand, normal larvae were always found only at fairly close quarters. The attacks on them were never made with the eagerness displayed against inverted preys, and in some cases only after marked hesitation. To those who witnessed these tests, this difference constituted impressive evidence for the protective value of countershading.

Now in the controls with painted larvae, we never detected any difference in the bird's behaviour toward normal and inverted larvae. This supports the conclusion that the excess of inverted victims among unpainted larvae is due to countershading, and not to obstruction of the bird's view by the twig.

A further question of some interest is whether the protective value of countershading is the same in all prey species investigated, and whether all Jays are deceived to the same extent by this camouflage. At first sight, Table IV may seem to suggest a negative answer on both points, but no conclusion regarding them should be based on our data for the following reasons. (1) Learning processes have great influence on the protective value of a camouflage against an individual predator (De Ruiter, 1952a, 1953). Now Dee was used in a far greater number of experiments than either Minstrel or Jean, and found more larvae than the other two Jays together. This may be the reason why countershading appears less effective against Dee. The following fact agrees with this view. The majority of the tests with *tiliae* were made when Dee was still inexperienced, and only a few more were made later at long intervals. Now *tiliae* is the only species in which countershading proved effective against Dee. (2) The majority of the data on *ligustri* were derived from one long uninterrupted series of tests on Dee, made when this bird was very experienced. Therefore, there is no reason to assume that the countershading of this species is less effective than, *e.g.*, that of *vinula.* (3) For a different reason the same applies to *versicolora.* The experiments on this species were made at the beginning of the season, when the birds had just been moved from their winter quarters in the laboratory to the aviary. Probably owing to this circumstance their searching was very little active during the *versicolora* tests. No reliance should be placed on this series.

Nevertheless, differences in the effectiveness of countershading against various predators will undoubtedly exist. We found some evidence for this in our experiments with Chaffinches. The number of captures obtained in this series was too low to justify any conclusion:

	I	N
ocellata	6	4
vinula	4	3

This may be connected with the fact that the Chaffinches, though known to catch such large larvae in nature occasionally, often seemed somewhat reluctant to attack them. The salient point, however, was the difference in hunting technique between Chaffinches and Jays. The latter, especially when hungry, make a rapid survey of a large area, and unless something at once attracts their attention, hop or fly on. Chaffinches, on the other hand, move slowly, making a minute search of areas with a much smaller radius. Our observations indicate that, if a caterpillar is present within this radius, it makes little difference whether it is in inverted or normal attitude. Of course, this does not mean that countershading is entirely ineffective against Chaffinches. The direction in which a finch will move on will be determined largely by the attractiveness of the things lying just outside the area it is searching at a given moment. A conspicuous larva may then turn the bird's attention to a direction which it would not have taken if the larva was camouflaged. An additional point of interest was that qualitative observations indicated that the Chaffinches were more afraid of the conspicuous inverted larvae than of the less formidable looking normal ones.

We cannot form an adequate picture of the ecological importance of graded pigmentation even to a single population of one countershaded species until we know its effect on each of the visual predators acting on the population, and the share of each predator in the total mortality. However, the data here presented enable us to conclude that countershading to some extent protects caterpillars from Jays, and probably from avian predators in general.

IV. THE USE OF SHADE AS A RECOGNITION MARK

The experiments to be described in this chapter were designed to determine whether the certainty with which Jays distinguish between flat and cylindrical objects of the same colour and outline is smaller when the cylindrical object is countershaded than when it is non-graded. I first trained the birds, when given the choice between two models, to look for food behind one (the "positive" model) and not behind the other (*e.g.*, behind a flat model, and not behind a cylindrical one). Once this conditioning had been established, I made discrimination tests in which the bird was given the choice between a pair of models, one of which was countershaded, the other being either cylindrical or flat.

The models (plate IV) were cigar shaped and 6 inches long. They were coloured grey with charcoal sprayed with a fixing agent. The background against which the birds viewed the models consisted of paper of the same shade of grey. I found it very difficult to make a satisfactory countershaded cylindrical model, and have certainly not achieved a result comparable, *e.g.*, to the *ocellata* larva. In nearly all experiments I used the same countershaded model, my best effort. This entailed the danger that the birds might learn to refuse this model, behind which no reward was ever offered, with the aid of accidental recognition marks. However, our conclusions, being based on positive reactions to this model, could not be invalidated by such conditioning. Of all other models, we used several different copies in random succession. The order in which a given type of model was offered on the left or right was also randomised. The same type was never given on the same side for more than four times in succession.

The food boxes were so small as to be entirely hidden behind the models, and so high that the Jay had to stretch a little to see the reward, if any. The reward (a mealwrom) was therefore invisible to the Jay until the bird had come up to the box, except in the rare cases when it flew high up and looked into the box from a distance. A bird was said to have made a choice only when it had actually looked into one of the food trays. The mealworms were killed in order to prevent them from making audible movements. The birds were never punished for "wrong" choices. They could see all movements of the experimenter during the preparation of the test. Therefore, I was very careful to keep the reward hidden from them, and to make exactly the same movements over both food trays, whether or not a reward was put in.

I soon found that the clearest results would be obtained if the Jays were compelled to make their choice at a considerable distance from the models. Fig. 7 gives the groundplan of the set up devised for this purpose. From one of the living-cages the bird could be admitted through a trapdoor B into C. The gateway D was so low that the bird could not fly into E. E itself was divided into two passages by means of a screen. All walls and screens were made of wire netting. Perches were provided in C, but not in E.

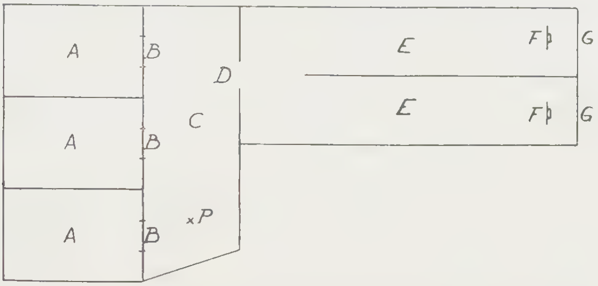

Fig. 7. Ground-plan of the set up of the discrimination tests.
A: living-cage; B: trapdoor: C: passage; D: gateway; E: passage divided by screen; F: model with food box; G: grey background. Scale 1:45.

The experiments were made in a darkened room, the source of light consisting of a fluorescent tube at a height of 80 inches above the food boxes, and a 200 W bulb at the same height over the spot marked P in fig. 7. Both lamps were screened with transparent paper. The countershading of the graded model was especially adjusted to this illumination.

Two Jays, called Samson and Delilah, were used in these tests. They had been taken from the nest about 10 months before, and been kept in captivity, first in the aviary at Wytham, later in the laboratory. Both were in good condition though their plumage had suffered somewhat from contact with the wire netting. The birds were only used when evidently hungry.

I first trained the birds to expect food behind a flat model, not behind a cylindrical one, and therefore to choose the former. This took rather a long time. Only after about 60 tests, each bird had reached a fairly constant level of performance, at which about 90 % of the choices were correct. The difference between this learning and the flashlike conditioning sometimes seen in Jays under other circumstances

(De Ruiter, 1952a, 1953) is very striking. There were no important differences in performance between Samson and Delilah.

It was still conceivable that, in spite of all precautions, the birds were guided in their choice not by the models but by some direct perception of the mealworm. Therefore, as soon as the preference for flat appeared to be established, I interspersed controls at irregular intervals among the conditioning tests. In these controls, the same choice was offered, but without reward. The results of the controls were not different from those of the conditioning tests:

	conditioning model chosen:		control model chosen:	
	flat	round	flat	round
Delilah. . . .	115	25	28	2
Samson. . . .	73	6	20	1

After more than 250 conditioning tests, the actual experiments were begun. Of course, the conditioning was also continued in the following period, and no reward was given in the experiments.

1. *Countershaded versus flat.* When given the choice between a flat model and a graded cylinder, the birds preferred the flat model just as much as in the controls, where the cylinder was non-graded:

	experiments		controls	
	flat model	graded cylinder	flat model	non-graded cylinder
Delilah. . . .	9	1	12	1
Samson. . . .	10	0	10	2
Total	19	1	22	3

Neither the numerical result, nor observations on the time it took the Jays to decide in the two cases, or on other aspects of their behaviour gave the least suggestion that they might confuse flat model and graded cylinder with each other. For fear of negative conditioning against the countershaded model I soon abandoned these tests in favour of another series.

2. *Countershaded cylinder versus non-graded cylinder.*

The ratio of "graded" to "non-graded" choices in these tests is not significantly different from that of "flat" choices to "round" choices in the controls. This suggests that indeed countershaded cylinder and flat model were to some extent similar to our birds. Yet there was one

	experiments			controls		
	graded cylinder	non-graded cylinder	no choice	flat model	non-graded cylinder	no choice
Delilah	10	1	4	15	1	0
Samson	8	2	12	23	2	0
Total	18	3	16	38	3	0

striking difference between experiments and controls in this series. In the experiments, the bird often did not look in the food trays at all ("no choice"). Of course, this was due to the birds' becoming negatively conditioned to the countershaded model as well. It is interesting that even in these cases a slight preference for the graded model above the non-graded cylinder was noticeable. Even when no choice was made the bird often entered one or both of the passages of E for some distance. Now as a rule, it came closer to the countershaded model than to the non-graded cylinder:

	nearer to		
	graded cylinder	non-graded cylinder	distances equal
Delilah	2	1	1
Samson	9	1	2
Total	11	2	3

The fact that the Jays preferred the graded model in this series of experiments is not in itself a sufficient basis for the conclusion that they found this deceptively similar to the flat model. It might be argued that the birds were merely conditioned to avoid the non-graded cylinder, but that they would accept any other model. However, this objection can be met. In the first place, if the birds would react to only one model, instead of basing their choices on a comparison between the pair offered, it seems more likely, in view of the fact that wrong choices were never punished, that they would react to the positive rather than to the negative model. Secondly, we have just seen that the birds, far from accepting any model except the non-graded cylinder, discriminated strongly between flat model and countershaded cylinder. Finally, the third and fourth series of tests discussed below show that the criticism does not apply in a very closely related case.

Therefore, the best interpretation of the results of this series seems to be that the birds preferred the graded model to the non-graded cylinder because the former was more similar to a flat model, though not sufficiently so to confuse the birds when given the choice between flat and countershaded-round.

The number of choices in each of the above series was small, and further extension of the experiments seemed desirable. However, the signs of negative conditioning to the countershaded model were too unmistakable to be disregarded. Therefore, I made two further series of tests with another type of model.

3. *plain flat (positive) versus shaded flat.* In this series both models were flat, but one was shaded with charcoal so that, to the human eye, it looked as round as the non-graded cylinder. It was remarkably more easy to shade a flat model than to countershade a cylinder. Therefore, I made several copies of the shaded flat model, which were used in random order so as to avoid conditioning to accidental characters.

	experiments			controls		
	plain flat	shaded flat	no choice	flat model	non-graded cylinder	no choice
Delilah	10	1	0	10	0	0
Samson.	10	0	0	10	0	0
Total	20	1	0	20	0	0

4. *shaded flat (positive) versus plain flat.* In this series, I had first reconditioned the birds, so that they now preferred the round instead of the flat model. This took about 80 conditioning tests. Once this conditioning had been sufficiently established, I began to intersperse controls and experiments, both, as usual, without reward. The birds were again given the choice between a flat model and a shaded flat one in these experiments.

	experiments			controls		
	shaded flat	plain flat	no choice	non-graded cylinder	flat model	no choice
Delilah	6	0	2	8	0	0
Samson.	8	0	0	8	0	0
Total.	14	0	2	16	0	0

In combination, these results do not seem open to any other interpretation than that to our Jays the shaded flat imitations of cylinders were deceptively similar to the really three-dimensional object. After the completion of these tests, I found that BENNER (1938) and SZYMANSKI (1920) had obtained similar results in studies on space perception in the domestic fowl.

Undoubtedly shade is but one of the clues used by Vertebrates in the perception of solidity (WALLS, 1942). Nevertheless, the evidence presented in this chapter indicates that Jays can be to some extent misled as to the shape of an object by its shading. Therefore, countershading must have protective value to any of their preys that in its general coloration resembles some inedible flat object, common in the prey's natural environment, *e.g.*, to a caterpillar having the same colour as the surrounding leaves.

A more general problem is, whether, apart from camouflage, three-dimensionality is one of the characters determining the releasing value of a prey for feeding in its predators. No data seem to be available on this point. However, interesting observations in a related field show that escape reactions in birds can be released with flat predator models only if these models are shaded (HARTLEY, 1950; NICE and TER PELKWIJK, 1941). In view of this, it seems possible that solidity will be found to add to the releasing value of a prey. In that case countershading will even protect preys that differ in colour from their environment from all enemies that judge roundness by shade.

V. THE APPLICABILITY OF CAGE EXPERIMENTS ON THE VALUE OF CAMOUFLAGE

Experiments on the survival value of camouflage take a great deal of time. Therefore, it is important that they be so designed that the maximum possible information can be extracted from the data obtained. We have seen that the form in which the results of such experiments are usually given is unsatisfactory from a quantitative point of view (p. 324). We shall now discuss another measure which may have more promising applications to some ecological and ethological problems.

The main problem of ecology is to account for changes in population numbers, and, in the case of polymorphic populations, for changes in the relative frequencies of the constituent types. The latter problem is especially important from the evolutionary point of view, such changes in relative frequencies being a basic process of evolution. Although few cases have been sufficiently analysed, there can be no doubt that changes in the composition of polymorphic populations will always be the resultant of many environmental influences. This complex can only be unravelled by investigating the effect of each influence separately. This involves great problems, as evidenced *e.g.* by the work of FISHER, FORD and SHEPPARD (SHEPPARD, 1953), and as a rule it will be impossible to make all the required observations in the field. It may therefore be asked how the results of experiments can be related to the processes occurring in nature, and we shall now make some remarks on this problem for the special case of the influence of predators on a population dimorphic with regard to camouflage.

In this case, we must determine the share of differential predation in the causation of shifts in the composition of the population. To simplify the discussion let us assume that predation is the only mortality factor operating. As a measure of the degree of differential predation in a dimorphic population we shall use the ratio E of the percentages of the individuals of each type that escape predation from the beginning of the generation until after the completion of reproduction. The relation of E to the selection coefficient s as used in evolutionary theory (HALDANE, 1924; WRIGHT, 1931) is simple. For instance, if the reproductive potential of individuals of both types is the same,

$$E = \frac{1}{1 - s}.$$

It may be noted in passing that the "selection index" used by DICE (1947, 1949) to express the results of his experiments on the camouflage of rodents is not identical to our s. In fact, his index is calculated only from the numbers of the two types of prey captured, and therefore open to the objection raised above (p. 324).

In order to determine E, we must study all predators acting on the population. However, we shall here restrict ourselves to the consideration of a single individual of one predator species. Let the frequencies at which the predator captures preys of types A and B be f_A and f_B, respectively, when the population density of each of these preys is unity. Let us further assume that the frequency of captures of preys of a given type is proportional to the population density of this type.

We then find for the decrease $-dP_A$ over a short time dt in the number P_A of preys of type A present in the hunting territory of the predator

$$-dP_A = f_A \cdot \frac{P_A}{S} \cdot dt,$$

where S is the size of the territory.

Hence, if the number of type A preys present at the start of an observation is P_A^o, and the number left after the predator has hunted for a time t is P_A^t, we find by integration

$$\frac{P_A^t}{P_A^o} = e^{-\frac{t}{S} \cdot f_A}, \quad \dots\dots\dots\dots \quad (1)$$

where e is the base of natural logarithms ($e = 2.718\dots$). If we make t equal to the whole time T spent hunting by the predator during the life of the generation of preys, so that P_A^o is the number of preys present at the beginning of the generation, and P_A^T that left at the end, we find for the prey population in the predator's territory:

$$E = \frac{e^{-\frac{T}{S}\cdot f_A}}{e^{-\frac{T}{S}\cdot f_B}} = e^{-\frac{T}{S}\cdot (f_B - f_A)} \quad . \ . \ . \ . \ . \ . \ . \ (2)$$

In principle, f_A and f_B can be measured in cage experiments. Of course, these experiments should be made under entirely natural circumstances. T and S will have to be determined in the field.

If we make an experiment with a sufficient number of preys of each type, and of sufficient duration, the average values of f_A and f_B can easily be determined from the percentages of survivors of each type by means of equation (1). Now in the literature on the value of camouflage, the results are commonly also given in the form of percentages of victims among the originally present numbers of preys of the types compared. Owing to practical difficulties, however, these data were almost never obtained in a single large experiment, but the percentages are arrived at by adding together the results of a number of tests, which as a rule are too small to be individually significant (*e.g.*, ERGENE, 1951). Of course, these percentages can only be used for the calculation of average f values if the duration of the individual tests was the same in all cases. Neither in our experiments, nor indeed in almost any other investigation has this condition been fulfilled. For that reason, I gave our results (chapter III) only in the form of numbers of victims.

It must be realised that to base a calculation of average f values on equation (1) means to assume that the frequency of captures is proportional to the population density of the preys concerned. This assumption is unproven. Hence, POPHAM's method of keeping the number of preys constant during the experiment (POPHAM, 1941), is preferable to the method so far considered, in which the number of preys decreases.

A further point of importance is that, if we calculate average f values from the total numbers of victims in a large experiment, we lose information on the fluctuations in frequencies which is important for the statistical evaluation of the results, and in connection, *e.g.*, with ethological problems. Hence, the best way to conduct the observations is to watch the predator continually, and to note the time at which individual captures are made. Of all papers on the subject, only one (POPHAM, 1941) contains tables from which such information can be derived, although its author makes no use of it in the way suggested here.

I want to stress that it is practically impossible that the simple equation (2) derived here will prove applicable without modification in a single concrete case. It is based on too many simplifying assumptions. However, each of these assumptions is open to verification. Perhaps, the result of this verification may sometimes be such that the formula can be modified accordingly. Even when, in a given case, the real situation proves too complicated for such mathematical treatment, the effort spent on the falsification of the assumptions will not be wasted, as each of them is a hypothesis of some ecological interest. In any case, from the ecological point of view the best way to express the results of experiments on the survival value of camouflage is to give data on the frequencies of captures and on the population density of the preys in the cage.

From the ethological point of view, camouflage in a prey is an adaptation to the releasing mechanism of feeding behaviour in its enemies: the prey cannot control the predators' hunger, but it can try to avoid eliciting their feeding activities. Consequently, data on the frequency of the feeding responses evoked by preys with varying degrees of camouflage may provide useful information on the properties of this releasing mechanism.

These data might shed some light, for instance, on such problems as the quantitative rules governing the co-operation of stimuli ("heterogeneous summation"; TINBERGEN, 1951), the supposed influence (PRECHTL, 1953) of internal factors on the selectivity of the releasing mechanism, and several others.

Feeding responses seem to be a particularly suitable subject for work in this field because they can be evoked with great frequency in all seasons by a very wide range of stimuli. Of course, the frequency of the captures of preys of a given type will depend not only on the releasing value of that type, but also on the number of preys per unit of space, and on the hunger of the predator. We can standardise the population density of our preys, but the effect of the predator's hunger can only be eliminated from our data by comparing the frequency of captures of the prey studied with that of the captures of simultaneously present preys of a standard type.

Therefore, we must always work with at least two types of prey in our experiments. This necessitates a special precaution. If two preys of different type are seen simultaneously, they may well influence each other's releasing values. Hence, the density of the preys should be kept so low that never more than one is seen at a time. It was shown by POPHAM (1943) that the density of the preys does indeed influence their relative releasing values. His data suggest that at sufficiently low densities this influence will no longer exist.

A predator will have a chance to detect a given prey only when within a certain distance of this prey. This distance will depend on the properties of both predator and prey. Therefore, for a given predator a prey may be said to be surrounded by a definite danger zone. Of course, in our experiments the danger zones of all preys should lie well within the space accessible to the predators. If part of the danger zone of a prey would be inaccessible, the risk run by this prey would be reduced accordingly. The radius of the danger zone can be estimated by observations on the behaviour of the predator. For a special case, a method to determine this radius was worked out by LAING (1938). In most of the published investigations, too little attention has been paid to this point. As the larger danger zones of the more conspicuous preys are more likely to lie partly outside the experimental space, this may at times have resulted in too low relative values for the risk run by these preys.

Further, in order to get consistent results, we must guard against the effects of adaptation (PRECHTL, 1953), and learning processes. For instance, all preys should consist of the same material and differ only in appearance, so as to exclude conditioned preferences. The test preys should not be made the staple diet of the predator, because monotony of diet might make them gradually less attractive.

It will be clear that many obstacles must be surmounted in work of this sort. In addition, because of the wide accidental fluctuations in frequencies of captures, conclusions can only be based on a large material. The choice of predators and preys is therefore very important. For instance, it would take a prohibitive amount of time to collect data on countershading suitable for the present purpose with the predators and preys used by us.

Nevertheless, in favourable circumstances, results of considerable value, from both the ethological and the ecological points of view, might be obtained in cage experiments on the value of camouflage. The prospects for further work in this field seem promising.

VI. SUMMARY

In this paper, evidence is put forward to show that countershading (for an explanation of the term, see p. 286) in caterpillars is an adaptation protecting the larvae from visual predators.

Our first argument in support of this conclusion is the fact that in their natural environment countershaded larvae always turn the dark side of their body towards the light, although there is wide variation among species in the anatomical substrates of the patterns and in the orienting mechanisms (chapter II).

Thayer's hypothesis as to the nature of the advantage conferred by graded pigmentation was confirmed by a series of cage experiments with Jays (*Garrulus glandarius* L.) as predators, and several species of countershaded caterpillars as preys. The results (chapter III, table IV) show that countershading has considerable protective value against this predator.

Finally, additional support for the hypothesis that countershading has a concealing effect was derived from some series of discrimination tests on captive Jays in which it was shown that these birds make use of shade in the identification of objects (chapter IV).

In the concluding chapter some remarks are made on the design of cage experiments and the applicability of their results to some ecological and ethological problems.

ZUSAMMENFASSUNG

Die vorliegende Arbeit bringt Argumente dafür, dass die Gegenschattierung (countershading, Begriffserklarung siehe S. 286) bei Lepidopterenraupen eine Schutzanpassung gegen optisch reagierende Raubfeinde darstellt.

Drei Tatsachen stützen diese Schlussfolgerung:

(1). Unter natürlichen Bedingungen drehen gegenschattierte Raupen immer ihre dunkle Körperseite dem Lichte zu, obwohl das morphologische Substrat der Gegenschattierung und die Orientierungsmechanismen im Raum artlich stark differieren.

(2). In einer Serie von Käfigversuchen boten wir Eichelhähern (*Garrulus glandarius* L.) verschiedene Arten gegenschattierter Raupen als Beute an. In Ûebereinstimmung mit Thayer's Hypothese erbrachten unsere Versuche den Beweis für die beträchtliche Schutzwirkung der Gegenschattierung.

(3). In einigen Serien simultaner Wahlversuche sahen wir, dass die Eichelhäher zum Erkennen von Objekten, Schatten als ein Merkmal gebrauchen.

Einige Bemerkungen über die Methodik von Käfigversuchen und die Bedeutung der damit gewonnenen Ergebnisse für ökologische und ethologische Probleme bringen wir im Schlusskapitel.

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THE CHEMICAL COMPOSITION OF THE HAEMOLYMPH IN PERIPLANETA AMERICANA

WITH SPECIAL REFERENCE TO THE MINERAL CONSTITUENTS

by

K. VAN ASPEREN AND IDA VAN ESCH
(*Laboratory for Research on Biocides T.N.O.*[1])

The processes occurring in the animal body are reflected in the composition of the body fluids. On this principle human medecine has based the rather new science of clinical chemistry. The chemical and cytological analysis of blood, urine, cerebrospinal fluid, bile and several secretions has proved to be of the first importance for a good judgment of the nature of pathological processes and conditions. Deviations from normal metabolism can easily be detected since the concentrations of most chemical substances in the body fluids, in normal circumstances, vary within rather narrow limits. This especially applies to concentrations in the blood, which may be considered to reflect the chemical processes in the human body fairly well. Moreover, the blood constitutes a very important medium for these processes. It contacts, directly or indirectly, all cells of the body and thereby has a very great influence on the course of metabolism in these cells. By far the most investigations in this field have been performed on the human body fluids, but certainly the above considerations hold for the body fluids in other groups of the animal kingdom as well.

The purpose of our investigations has been to obtain an impression of the chemical composition of the haemolymph of *Periplaneta americana* L. This insect was chosen because it is used in our laboratory as an experimental animal in many of the investigations on the action of insecticides. We did not content ourselves with the determination of the average values but attempted as well to obtain information on the in-

[1] Vondellaan 6, Utrecht.

dividual differences. Moreover, we examined the changes in the chemical composition following disturbances of the normal conditions brought about experimentally. This was expected to give us some information on circulation, tolerance and regulation.

Several investigators collected data on the chemical composition of the haemolymph in insects. These have been summarized e.g. by Buck (1953) Wigglesworth (1950), Boné (1944), and Duchâteau, Florkin and Leclercq (1953). The last authors paid special attention to the mineral constituents and to the relation between mineral composition of the haemolymph and feeding habits or systematic position of the insects. Our work too was mainly concerned with the mineral composition since it is a well known fact that in many animals there are strong relations between mineral composition and excitability of nerves and muscles. To elucidate such relations is of the utmost importance for the physiological investigations of insect nerves and muscles and indirectly for the research on the insecticidal action of several compounds.

I. EXPERIMENTAL TECHNIQUES

Animal material. Our determinations and experiments have all been performed on the American cockroach, *Periplaneta americana* L. The experimental animals were obtained from the Zoological Gardens "Artis" at Amsterdam. In our laboratory the animals were kept at 29 °C. They were fed on a mash, consisting of 10 parts of wheat meal, 9 parts of whole milk powder and 1 part of dried yeast, supplemented with vitamins A and C, mixed in water.

Only adults have been used, except in a few cases, where calcium and magnesium determinations were made in the haemolymph of last instar nymphs. It should be emphasized that the age of the animals on arrival in the laboratory was unknown.

Injection technique. The roaches were injected by inserting the injection needle between the sternites of the 5th and 6th abdominal segments and delivering, by means of an "Agla" micrometer syringe, an amount of fluid varying from 30 to 100 μl. The injection of such an amount of fluid in itself is quite harmless to the insects.

Haemolymph for analysis was collected in several ways. Sometimes antennae and legs were cut off by scissors and the haemolymph appearing on the cut surfaces drawn into a capillary pipette. In other cases haemolymph was obtained by puncturing with a blunt glass needle the thin exoskeleton where the prothoracic leg joins the thorax or by making a little hole at the ventral side of the abdomen between the sternites. In all cases nearly or completely clear haemolymph was obtained. The amounts which could be collected from a single individual varied from 10 to 50 μl.

Methods for the determination of sodium, potassium, and chloride. All methods to be described here, have been checked by performing determinations in solutions of known composition and in normal human sera.

Sodium. After dilution with distilled water the haemolymph was deproteinized with trichloroacetic acid. To the filtrate was added zinc-uranyl-acetate reagent and ethanol to precipitate the sodium as sodium-zinc-uranyl-acetate. The fluid was centrifuged, the supernatant liquid discarded and the precipitate washed three times with acetone saturated with sodium-zinc-uranyl-acetate. The precipitate was then dissolved in hot water and transferred to a small beaker. The amount of sodium-zinc-uranyl-acetate was then titrated electrometrically with sodium hydroxide solution. References: WEINBACH (1935); GORTER and DE GRAAFF (1947).

Potassium. Determinations were all made with a flame-photometer after precipitation of proteins by trichloroacetic acid. The smallest amount of haemolymph permitting reliable measurements of the potassium-concentration was about 100 μl. Therefore, in the case of potassium, no determinations could be performed in single individuals of the insect.

Chloride. Two methods were used, which were both quite satisfactory.

1. The haemolymph was deproteinized by addition of 90 per cent ethanol. After centrifugation the supernatant liquid was transferred to a small flask. After washing the precipitate once with 90 per cent ethanol and adding the washing to the flask, the chloride was titrated with silver nitrate using potassium chromate as an indicator. This method is essentially that of MOHR (ref. NOYONS, 1952).

2. A second method which was used successfully is that described in literature as Votoček's method. The haemolymph was deproteinized with trichloroacetic acid. The chloride in the filtrate was titrated with mercuric nitrate using diphenylcarbazone as an indicator. Ref. GORTER and DE GRAAFF, 1947.

Methods for the determination of some organic constituents. All methods, which will be described here, have been checked by performing determinations in solutions of known composition and in normal human sera.

Total nitrogen and Non-protein nitrogen were determined by a micro Kjeldahl method. Total nitrogen (T.N.) was determined by complete destruction of a very small amount of haemolymph with sulphuric acid. After addition of sodium hydroxide the ammonia was distilled into a solution of boric acid by way of a Parnas-Wagner apparatus and titrated with 0.02N hydrochloric acid. Non-protein nitrogen (N.P.N.) was determined in the same way after precipitation of proteins with trichloroacetic acid. (Unless large quantities of haemolymph are available, the determinations of N.P.N. are rather inaccurate. The estimation of N.P.N. in single individuals, therefore, is very difficult.)

Total Reducing Value was determined by the Hagedorn and Jensen method. The haemolymph was deproteinized with cadmium hydroxide and oxidized by an alkaline potassium ferricyanide solution. The excess of ferricyanide was measured by iodometric titration. This Total Reducing Value (T.R.V.) was expressed as glucose, but probably it is due only in part to glucose or even to sugars. No seperate determinations on fermentable and non-fermentable reducing substances have been made. References: ARIENS (1950); FUJITA and IWATAKE (1931).

Methods for the determination of calcium and magnesium. In a previous paper (VAN ASPEREN and VAN ESCH, 1954) we gave a very short description of a micro method for the determination of calcium and magnesium. As this method has not yet been published in more detail, we shall give a detailed description here. The method is based on the use of a chelating agent as introduced by SCHWARZENBACH et al. (1946) for the determination of several metals. The chelating agent, ethylenediamine tetraacetate (EDTA), has been proved to be very useful for the direct titration of calcium and magnesium, especially in the determination of water hardness and in clinical investigations of blood plasma. As, in our case, only very small amounts of fluid were available, we used a well known Linderstrøm-Lang microtitration technique (ref. GLICK, 1949).

Procedure. A small amount of haemolymph obtained from the roach as described above and varying from 5 to 20 μl, was drawn into a small glass pipette by capillary forces. The fluid was then blown out into a small titration vessel (capacity ca 500 μl), weighed and diluted with approximately 100 μl of distilled water.

In the case of the calcium titration ca 10 μl 4 N sodium hydroxide and ca 5 μl

0.4 per cent murexide solution were added immediately before the titration which was carried out with 0.004 N ethylenediamine tetraacetate solution (brought to pH 10.8 with sodium hydroxide) from a Linderstrøm-Lang microburette.

In the case of the magnesium titration ca 60 μl 0.1 N sodium hydroxide, ca 25 μl M ammoniumchloride-ammoniumhydroxide buffer solution and ca 5 μl 1 per cent eriochrome black T solution were added immediately before titration, which was performed as above.

The EDTA titration fluid was prepared according to HOLTZ (1951) by dissolving 1.488 gm of di-sodium ethylene diamine tetraacetic acid-dihydrate in distilled water. The solution was titrated with N sodium hydroxide to pH 10.8 and then made to 1 liter with distilled water. It is stable.

The murexide solution was prepared by dissolving ca 40 mg of murexide in 10 ml of distilled water. Since this material is unstable, the solution should be freshly prepared every few days.

The eriochrome black T solution was prepared as described by BUCKLEY, GIBSON, and BORTOLOTTI (1951). This solution is stable for many weeks if kept in a refrigerator.

Discussion of the method. At the pH of the titration the calcium-murexide complex shows a pink shade, whereas the calcium-free murexide solution is lilac blue. Murexide, therefore, is used as an indicator for the presence of unchelated calcium. The indicator for the presence of magnesium is eriochrome black T which forms a bright red complex with magnesium. In the absence of magnesium the dye assumes a blue colour. The rather faint yellow colour of the haemolymph did not interfere, except in a few cases, where dark brown pigments had developed after preservation of the haemolymph for more than one day.

The affinity of EDTA for calcium is much greater than for magnesium. The end point of the murexide titration, therefore, indicates that all the calcium has been chelated, whereas in the eriochrome black titration the colour shift occurs only when both the calcium and magnesium have been chelated. The difference between the amounts of EDTA used in both titrations can thus be used for the calculation of the magnesium content.

Calculations are very simple since one mole of EDTA chelates one mole of divalent cation. As, according to BUCKLEY, GIBSON, and BORTOLOTTI (1951), a period up to 45 seconds between drops of EDTA is required for the colour to become stabilized, the end point of the titration should be approached very slowly.

Reliability of the method. Several experiments were performed to test the reliability of the method.

1. Micro-determinations of calcium and magnesium, according to the above description, were carried out on solutions, containing varying amounts of calcium chloride and magnesium sulphate and on human sera, to which varying amounts of magnesium sulphate had been added. The results were compared with those obtained with macro-methods. From Table 1 it may be concluded that there is a good agreement of the data obtained by calculation, macro-determination and micro-determination.

According to Table 1 the standard deviations calculated for most series of parallel determinations are rather small and generally do not exceed 5 per cent of the average value.

2. Haemolymph was collected from several cockroaches and determinations were made in samples of this pooled haemolymph. This procedure was repeated several times and the standard deviations of all series of parallel determinations were calculated. Each series consisted of 2-8 determinations. For eight series of the micro-calcium titration the standard deviations averaged 5 per cent of the mean (18.6 mg calcium per 100 gm of haemolymph). For nine series of the micro magnesium titra-

TABLE 1 Determination of calcium and magnesium in solutions and human sera

	Determination of	Results, all expressed as M ± S.D.[1], in milligrammes/100 gram.			
		Calculated	Macro-EDTA-titr.	Micro-EDTA-titr.	Macro-oxalate prec.
$CaCl_2$-solution	Ca	—	9.2 ± 0.1 (5)	9.4 ± 0.6 (13)	9.1 ± 0.1 (2)
Human serum	Ca	—	10.5 ± 0.0 (2)	10.3 ± 0.1 (5)	10.6 ± 0.1 (2)
$CaCl_2$ + $MgSO_4$-solution	Ca	18.4	19.6 (1)	19.0 ± 1.8 (5)	—
	Mg	30.0	30.2 (1)	31.7 ± 1.2 (5)	—
$CaCl_2$ + $MgSO_4$-solution	Ca	18.4	—	17.6 ± 0.7 (3)	—
	Mg	15.0	—	16.3 ± 0.4 (5)	—
Human serum + $MgSO_4$	Ca	11.7	11.6 (1)	—	—
	Mg	36.8[2]	34.6 (1)	—	—
$MgSO_4$-solution	Mg	30.0	30.1 ± 0.1 (2)	31.6 ± 1.7 (8)	—
Human serum + $MgSO_4$	Mg	17.4[2]	16.2 ± 0.1 (2)	17.9 ± 0.8 (5)	—
Human serum + $MgSO_4$	Mg	17.7[2]	—	16.3 ± 0.8 (3)	—

In brackets: number of determinations

[1] M = Mean value; S.D. = Standard Deviation = $\sqrt{\frac{\Sigma d^2}{n-1}}$

[2] Calculated assuming that the Mg-content of the plasma is 3 mg/100 gram.

tion the standard deviations averaged 14 per cent of the mean (13.8 mg magnesium per 100 gm of haemolymph). This last value is rather high, for which two reasons may be produced: a. Magnesium concentrations are calculated from the difference between two titration values and therefore are liable to greater errors than the calcium concentration which can be titrated directly. b. Usually after the haemolymph has been collected some coagulation of cells and proteins occurs. By collecting most of the coagulate in one sample we were able to show that the magnesium content of the coagulate is distinctly higher than that of the clear serum. The calcium concentrations of coagulate and serum were not significantly different.

3. Duplicate determinations of calcium and magnesium were made by taking two samples of haemolymph successively from the same insect. This was repeated several times. On average the duplicate values differed by 9 per cent for the calcium and 12 per cent for the magnesium determinations.

4. Haemolymph was collected and micro- and macro-EDTA-titrations were carried out. There was a very good agreement of the results, the differences amounting to only a few per cent.

5. In two experiments 116 per cent and 89 per cent of magnesium sulphate added to samples of pooled haemolymph were recovered. Taking into account that each experiment includes several manipulations with small amounts of fluid, these results are reasonable.

From the results of the experiments described above, the conclusion can be drawn, that the titration in itself is reasonably accurate. The greatest errors are introduced by the manifold handling of the haemolymph. This, therefore, should be reduced as far as possible.

The calcium concentration being fairly constant, we felt ourselves justified, at least in a number of determinations, in omitting the murexide titration and in calculating magnesium concentrations by subtracting the average titration value for calcium from the value obtained with the eriochrome black titration. This of course introduces an error, but, since the number of manipulations is decreased, the accuracy of the titration is enhanced.

II. THE CHEMICAL COMPOSITION OF THE HAEMOLYMPH

The methods described in the preceding section have all been adapted to the small amounts of haemolymph which could be obtained from individual insects. By performing rather large numbers of determinations in single individuals we have been able to obtain data on the individual variation as well as on the average values. Table II shows the data obtained for sodium, potassium, chloride, calcium, magnesium, total-nitrogen, non-protein nitrogen, and total reducing value. The data for non-protein nitrogen, although giving a good impression of the average concentration are rather inaccurate with regard to the individual variability as expressed by the standard deviation. Apart from many determinations in single individuals several determinations have been made in pooled haemolymph, which are also presented in Table II.

Discussion. If we compare our results with those found in literature, we note a very good agreement in the data for sodium, chloride, and calcium, but large differences in the data for potassium, magnesium, and T.R.V. Differences may be due to several factors, such as differences in the previous history of the insects, environment, feeding conditions, race etc. Whether our data agree with those of literature, in our view therefore, could largely be a matter of chance. This is supported by a number of observations made after the data of the table had been collected. Thus the T.R.V., a year after the data of the table had been obtained, averaged about 500 mg per 100 gm of haemolymph, which is more than three times as much as quoted in the table (range 210–740). The total nitrogen, one year later, on an average proved to be considerably lower than according to Table II. The mean amounted to about 700 mg per 100 gm of haemolymph with very large individual differences. We are not, therefore, inclined to attach too much importance to the mean values obtained in our investigations and to those found in literature. Differences may be caused by the diet. TOBIAS (1948) proved, that by giving a leaf diet (lettuce) during 12–18 days preceding the chemical analysis of the haemolymph, the potassium concentration of the serum was increased with more than 50 per cent. Oral administration of concentrated potassium chloride solutions resulted in a more than 100 per cent increase of the potassium value. We

TABLE II Chemical composition of the haemolymph of *Periplaneta americana*
Concentrations all expressed in milligrammes per 100 gram of haemolymph

	Sex	Number of determinations	Method*	Mean ± S.D.	Range	Literature
Sodium	male	47	single	378 ± 59	247–500	350[1]
	female	45	single	332 ± 63	220–528	
	male + female	18	pooled	370 ± 55	264–540	
Potassium	male + female	32	pooled	31 ± 5	25–50	100[1]
Chloride	male	44	single	507 ± 43	423–660	504[3]
	female	49	single	518 ± 45	437–639	
	male + female	19	pooled	512 ± 32	454–588	
Calcium	male	43	single	17.4 ± 1.7	14.5–21.6	17 ± 3[2]
	female	31	single	18.1 ± 2.3	12.0–25.1	
	unknown	33	single	18.0 ± 1.6	15.2–21.2	
	nymphs	2	single	17.4		
	male + female	54	pooled	16.1 ± 2.1	12.2–23.6	
Magnesium	male	40	single	13.3 ± 3.5	7.0–22.8	7[1] 27 ± 4[2]
	female	43	single	13.7 ± 2.4	10.8–22.6	
	nymphs	4	single	12.5		
Total-Nitrogen	male	49	single	1041 ± 242	647–1664	
	female	43	single	1054 ± 230	683–1760	
	male + female	11	pooled	990 ± 250	670–1528	
Non-protein Nitrogen**	female	16	single	229 ± 82	140–483	
	male + female	11	pooled	227 ± 52	126–300	
Total Reducing Value** †	male	34	single	148 ± 42	80–276	65[4]
	female	36	single	141 ± 32	87–215	

* *Single* means that each determination was performed on the haemolymph of one individual insect.

Pooled means that each determination was performed on a sample of haemolymph collected from several insects.

† Data for Total Reducing Value expressed as mg glucose per 100 gm of haemolymph.

** In a later series of experiments strongly deviating results have been obtained; see Discussion below.

References: [1] Tobias (1948); [2] Clark and Craig (1953); [3] Munson and Yeager (1949); [4] Yeager and Fay (1935).

do not know the potassium concentration of the diet given in our laboratory and very little is known about the diet of the insects in the Zoological Gardens at Amsterdam. Therefore, the possibility of the diet being a cause of differences cannot be excluded. Nevertheless we feel that the differences between our values for potassium and those given by Tobias probably are too large to be explained by dietal factors only. As a result of the very low potassium values the sodium/potassium ratio in the whole haemolymph of our insects was about 20. This very high value, according to BONÉ (1944), is characteristic of carnivorous and aquatic insects. For a pantophagous insect like *Periplaneta americana* a much lower ratio would be expected. According to DUCHÂTEAU, FLORKIN, and LECLERCQ (1953) high values of the sodium/potassium ratio, as occurring in many groups of animals, are mostly found in the primitive groups of insects, whereas low sodium/potassium ratios are to be considered as biochemical specializations.

Diet could have played an important part in the great variation of our T.N.-values too. We observed a tendency of the T.N.-concentrations to increase if the insects were kept in our laboratory for a longer period of time. This, perhaps, may be the result of the rather large amounts of protein-rich food ingested.

The large differences between the T.R.V. given by YEAGER and FAY (1935), the data of Table II, and those found in our later investigations (respectively 65, 145 and 500 mg glucose per 100 gm of haemolymph) are likely to be caused by differences in diet and life conditions though we have no definite proof of it.

With regard to the magnesium concentrations our data differ greatly from those given by TOBIAS (1948), which are much lower, and from those given by CLARK and CRAIG (1953), which are considerably higher. In a former paper (VAN ASPEREN and VAN ESCH, 1954) we expressed our view that the dry-ashing of the haemolymph, as used by both authors, may lead to erroneous results because by this procedure organic phosphorus is converted to inorganic phosphates which may interfere. However, in the light of the large differences found for potassium and some organic constituents with similar methods, we cannot exclude the possibility that differences in the animal material have played a part.

The values for calcium and chloride in our investigations show relatively small variations as expressed by the rather small standard deviations and moreover they agree quite well with those found in literature.

In a preceding paper (VAN ASPEREN and VAN ESCH, 1954) calcium and magnesium concentrations were also given for two other species of Blattaria (*Periplaneta australasiae* and *Blabera fusca*). From these data it could be concluded that the interspecific differences are rather small and that the calcium/magnesium ratio is about the same in all three species. If both calcium and magnesium concentrations are expressed in molarities, this ratio is 0.79 in *Periplaneta americana*, whereas CLARK and CRAIG (1953) found a ratio of only 0.37. This, once more, is a warning against drawing far reaching conclusions from such rather uncertain data. In correlating the ionic composition of the body fluids with feeding habits, systematic position etc. much more attention should be paid to variations resulting from several causes.

From Table II it may be concluded, that in general the individual variability is much less for the mineral than for the organic constituents and especially in the case of calcium and chloride the individual differences are small. This might perhaps indicate the importance of rather fixed relations and stable conditions with regard to the mineral composition of the haemolymph. In the third section of this paper we shall deal with this problem in more detail. The differences between the concentrations found in the two sexes do not appear to be significant.

The ion balance shows a great resemblance to that in human plasma. The total cation titre of 183 milliequivalents (sodium 157, potassium 8, calcium 8, magnesium 10) is 79 per cent balanced by 144 anionic milliequivalents chloride. According to GLASER (1925) the pH of the haemolymph of *Periplaneta americana* is 7.5–8.0. The total protein content of the haemolymph being rather high, proteinates are very likely at this pH to make a major contribution to the residual 39 negative milliequivalents. Bicarbonates and phosphates probably do not play an important part in the cation-anion balance.

Binding of cations to proteins should be taken into consideration. Sodium and potassium have both been determined after deproteinization of the haemolymph, as is usual in human clinical chemistry. As, however, rather high concentrations of trichloroacetic acid were used it is very unlikely that protein bound fractions of these minerals could have been eliminated in this way. The data obtained for all cations, in our view, represent the total concentrations in the haemolymph of the insects.

The fact should be emphasized, that we did not distinguish between whole haemolymph and haemolymph serum as was done by TOBIAS (1948). The haemolymph always proved to be an almost or completely clear fluid. Some coagulation occurred on standing. This was most probably a clotting of proteins and haemocytes, but the volume of the clot was very small. Haemocyte counts in 32 females and 28 males averaged 67,000 ± 18,000[1] and 67,000 ± 16,000[1] per μl respectively. From these data the conclusion can be drawn that the total cell volume of the haemolymph is very small. Therefore, only small differences between whole haemolymph and serum can be expected. In our view the differences up to 40 per cent as found by TOBIAS (1948) are quite inexplicable.

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[1] Standard deviation $= \sqrt{\frac{\Sigma d^2}{n-1}}$

III. TOLERANCE AND REGULATION

In the preceding section we have dealt with the normal chemical composition of the haemolymph. Special attention has been paid to the individual variability of some organic and the most important mineral constituents. The rather small individual differences with regard to the mineral constituents, especially calcium and chloride, led us to suggest that it is important for the animals to maintain more or less fixed relations and conditions. It will be the purpose of this section to describe a number of experiments, in which these relations and conditions were disturbed in order to get a better insight into the potentialities of tolerance and regulation. The disturbance of normal conditions was achieved by injecting varying amounts of distilled water, simple salt solutions or "physiological" salt solutions of varying composition. In a number of cases insecticidal emulsions were injected to bring the insects into very abnormal physiological conditions.

Experiments were all performed in the following way. The insects were divided into a number of groups, each group consisting of from 6 to 40 animals. The insects of one of these groups were not injected and served as controls. The others were all injected with the same amount of injection fluid. After a certain interval of time haemolymph for analysis was collected from one of the groups and this was repeated with the other groups at later times. Haemolymph was taken only once from each insect.

I. INJECTION OF DISTILLED WATER AND INSECT RINGER SOLUTION; DETERMINATION OF SODIUM, CHLORIDE, TOTAL NITROGEN, AND NON-PROTEIN NITROGEN

The Insect Ringer solution used was composed of 9.32 gm NaCl, 0.77 gm KCl, 0.50 gm $CaCl_2$, 0.18 gm $NaHCO_3$, 0.01 gm NaH_2PO_4, and distilled water to 1 liter. The composition of this Ringer solution and that of haemolymph are compared in Table III.

TABLE III

The composition of Insect Ringer solution and haemolymph of *Periplaneta americana*

Element	Insect-Ringer-Solution	Haemolymph
Sodium	162 millimol./liter = 372 mg/100 ml.	360 mg/100 ml.
Potassium	10.3 millimol./liter = 40 mg/100 ml.	30 mg/100 ml.
Calcium	4.5 millimol./liter = 18 mg/100 ml.	17 mg/100 ml.
Magnesium		13 mg/100 ml.
Chloride	178 millimol./liter = 632 mg/100 ml.	512 mg/100 ml.

In this series of experiments 77 μl of distilled water or Insect Ringer solution was injected and haemolymph was collected from legs and antennae after varying intervals of time. The results are presented in Table IV, where the concentrations are expressed as percentages of the values found for the haemolymph of control groups.

TABLE IV Injection of distilled water and Ringer solution
Concentrations all expressed as percent of the controls

Injected 77 μl.	Distilled water			Ringer-solution		
	Interval of time[1]			Interval of time[1]		
	0–10 min.	60 min.	150 min.	0–10 min.	60 min.	150 min.
Sodium	82 (2)	98 (3)	97 (1)	92 (2)	100 (1)	107 (1)
Chloride	91 (2)	89 (2)	115 (1)	95 (2)	110 (2)	100 (1)
Total-Nitrogen	74 (1)	100 (2)	87 (1)	68 (2)	81 (2)	79 (1)
Non-protein Nitrogen	90 (1)	93 (2)	108 (1)	77 (2)	90 (2)	104 (1)

In brackets the number of observations from which the mean values given in the table are calculated.

[1] "Interval of time" is the interval between the injection and the collection of the haemolymph.

No abnormalities in the behaviour of the insects were observed after injection of these fluids.

Discussion. For the interpretation of these results a good knowledge of bloodvolume, circulation time and time necessary for complete mixing of injected fluid and haemolymph is very important. According to YEAGER and MUNSON (1950) the blood volume of adult *Periplaneta americana* is about 20 per cent, whereas WIGGLESWORTH (1950) gives a value of only 6 per cent. For several reasons we prefer the first value. It should, however, be kept in mind that probably large differences may occur. We attempted to determine the blood volume by injecting Evans' blue solution, but very irregular results were obtained. This was most probably due to adsorption of the dye by the tissues. The mean weight of the cockroaches in our investigations was about 1 gm, so the blood volume may be approximately 200 μl.

If no regulation took place, the injection of 77 μl of distilled water would result in a decrease in concentration to about 75 per cent after complete mixing. The same decrease may be expected for Total Nitrogen and Non-protein Nitrogen after injection of 77 μl of Ringer solution. Such a dilution is indicated only in the case of Total Nitrogen and immediately after injection for sodium and Non-protein Nitrogen. The results suggest strongly the occurrence of regulation processes in the first hours after injection in the case of sodium, chloride and Non-protein Nitrogen. This regulation is not achieved by removal of water from the haemolymph as in this case Total Nitrogen values would also be restored. As we did not feel these results to be conclusive, further experiments were performed.

2. INJECTION OF ABNORMAL INSECT-RINGER SOLUTIONS; DETERMINATION OF SODIUM AND CHLORIDE

Only a small number of experiments of this kind was performed. In all cases 77 μl was injected and haemolymph collected after one hour from legs and antennae. Injection of Ringer solutions, in which KCl or $CaCl_2$ had been substituted by an equivalent amount of NaCl did not affect the sodium and chloride concentrations. If NaCl was replaced by an equivalent amount of KCl, the sodium concentration was lowered to 73 per cent, whereas Cl was unaffected. Injection of a Ringer solution, to which 1.28 per cent KCl had been added, brought about only a small increase of chloride concentration. The sodium concentration in one case was unaffected and in another case it was considerably increased.

The injection of Ringer solutions with very high potassium concentrations (670 and 710 mg/100 ml), as described above, generally resulted in paralysis. Movements in the insects became very slow and most animals were lying on their backs for a long time. After 5 to 6 hours recovery started. After a lapse of 24 hours 3 out of 10 insects were dead, the remaining 7 were quite normal. No abnormalities were observed after the injection of potassium free or calcium free Ringer solutions.

3. INJECTION OF DISTILLED WATER AND CONCENTRATED CALCIUM CHLORIDE SOLUTIONS; DETERMINATION OF CALCIUM

Haemolymph was collected from several parts of the insects as described before.

The concentration of calcium in the thoracal haemolymph was only slightly affected by the injection of 80 μl of distilled water. If, however, the haemolymph was collected from the abdomen, an initial decrease of the concentrations to about 55 per cent was observed 7 to 30 min. after the injection. After 60 min. and 145 min. respectively 79 per cent and 83 per cent of the normal concentration was found.

A large number of experiments were performed, in which 30 μl of a concentrated calcium chloride solution, containing 219 mg calcium per 100 ml (54.8 mMol), was injected. Haemolymph was collected from the abdomen or from thorax, legs and antennae. Fig. 1 shows the results. All plots in this figure are mean values calculated from 3–12 determinations. The Standard Deviations for the individual observations made for each plot averaged 23 per cent of the plotted mean value. The Standard Errors of the plotted mean values ranged from 4 to 15 per cent, averaging 9 per cent.

Discussion. Assuming as we did that the total volume of haemolymph is 200 μl, the concentration resulting from the injection of 30 μl of this calcium chloride solution would be about 44 mg per 100 ml. This value would be reached after complete mixing of haemolymph and injected fluid, provided that no regulation took place (we may call this the *simple mixing level*). From the graphs of fig. 1 it can easily be seen that complete mixing occurs only after about one hour. At that time a calcium concentration of about 27 mg per 100 ml is reached. This means either that calcium has shifted from the haemolymph to the tissues or that a calcium free solution or water has been transferred from the tissues to the haemolymph. In either case some kind of regulatory process has to be present.

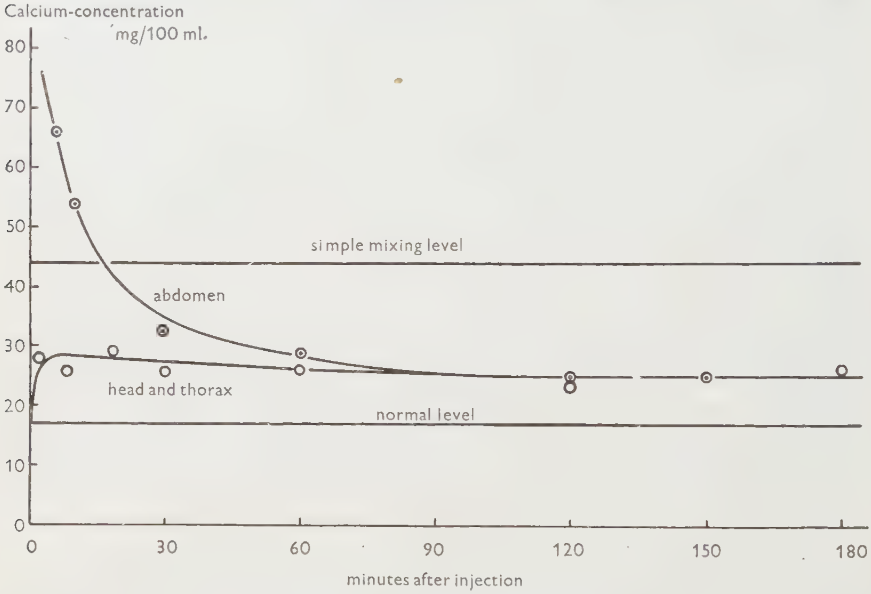

Fig. 1. Calcium concentration after injection of 30 μl of calcium chloride solution containing 219 mg calcium per 100 ml.
⊙——⊙ haemolymph collected from abdomen
○——○ haemolymph collected from thorax, legs and antennae.

In order to find out whether or not the haemolymph could have been diluted by watertransport from the tissues, chloride and Total Nitrogen determinations were made in the haemolymph at several times after injection of the calcium chloride solution. The chloride and T.N.-values found 60 and 150 minutes after the injection were only slightly lower than those of the controls (chloride 96 ± 7 per cent; T.N. 96 ± 17 per cent). Most probably, therefore, regulation is achieved by removal of calcium from the haemolymph. We are quite ignorant as to where and how this calcium regulation is brought about.

Most remarkably the calcium concentration in the thoracal haemolymph is increased to about 27 mg per 100 ml immediately after the injection and this level is maintained during the whole regulatory period. The interpretation of these results is very difficult because very little is known about the circulation and distribution of haemolymph in the body. We did some experiments, in which dyes (filtered solutions of Indian ink or Evans' blue) were injected into the abdomen. They were seen to spread within a minute through the whole body, but measurement of the colour intensity revealed that there was no uniform distribution, even after a long period of time.

Similar circulatory factors may affect the results obtained after injection of distilled water or salt solutions and could give an explanation of many of the data obtained in our experiments. It might be suggested that the rapid spread of salts or dyes in the first minute or even the first seconds after the injection is caused by an increase of pressure in the abdomen as a consequence of the injection.

4. INJECTION OF DISTILLED WATER AND CONCENTRATED MAGNESIUM SULPHATE SOLUTIONS; DETERMINATION OF MAGNESIUM

Two experiments have been made, in which 80 μl of distilled water was injected and haemolymph was collected from the abdomen. The results were somewhat irregular, but there was an indication that the very low concentration (6.5 mg 100 ml), observed after about 7 min. is increased during the following 30–60 minutes, without, however, reaching the normal level.

In several experiments the insects were injected with 30 μl of a magnesium sulphate solution containing 300 mg magnesium per 100 ml (125 mMol). Magnesium determinations were performed on the samples of haemolymph taken from the abdomen after varying periods of time. The results can be found in Fig. 2.

Discussion. The magnesium concentration resulting from simple mixing of the haemolymph (volume taken as 200 μl) and injected fluid, can easily be calculated. This value ("simple mixing level") is about 50 mg per 100 ml. The magnesium concentration actually falls below this level, but not as rapidly and distinctly as has been found for calcium in the preceding experiments. This may be caused by the very large amount of magnesium injected. It should be emphasized, however, that the animals all behaved quite normally. This, in itself, is very surprising, as in many animals, magnesium concentrations as high as those found in our experiments have strongly narcotizing effects which are antagonized by calcium. LEVENBOOK (1949) injected magnesium into the haemolymph of adult locusts and found that it rapidly produced a cataleptic condition. The insects recovered after a subsequent injection of calcium, which, if injected alone, would have been fatal. So, both calcium and magnesium are highly toxic for locusts, but both ions together are non toxic by reciprocal antagonism. This certainly is not true for *Periplaneta americana*. No toxic effects of either calcium or magnesium were observed at the concentrations studied or after injection of 60 μl of the concentrated solutions, which is twice as much as used in the experiments.

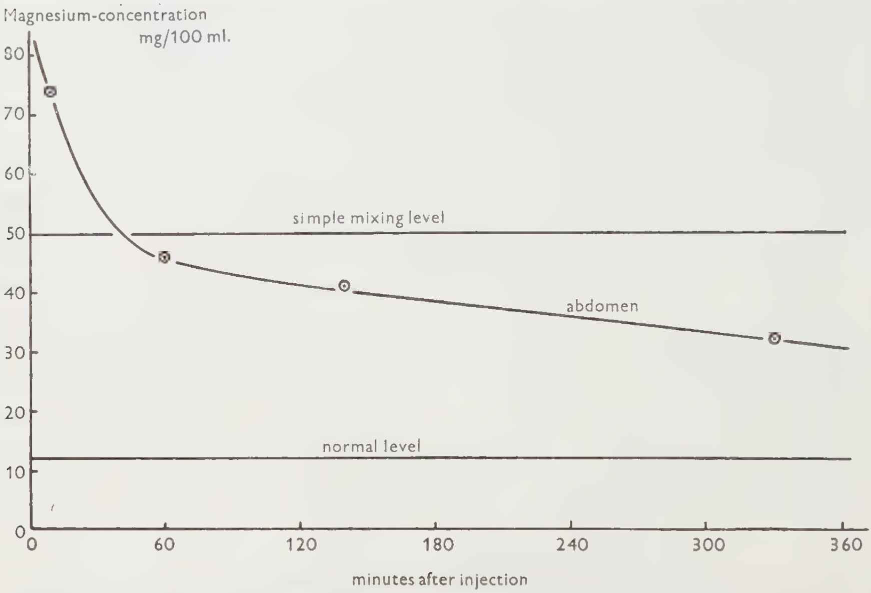

Fig. 2. Magnesium concentration after injection of 30 μl of magnesium sulphate solution containing 300 mg magnesium per 100 ml.

5. INJECTION OF ETHYLENEDIAMINE TETRAACETATE SOLUTIONS; DETERMINATION OF CALCIUM AND MAGNESIUM

The object of the injection of distilled water described under 3 and 4 was to lower the calcium and magnesium concentrations in the hae-

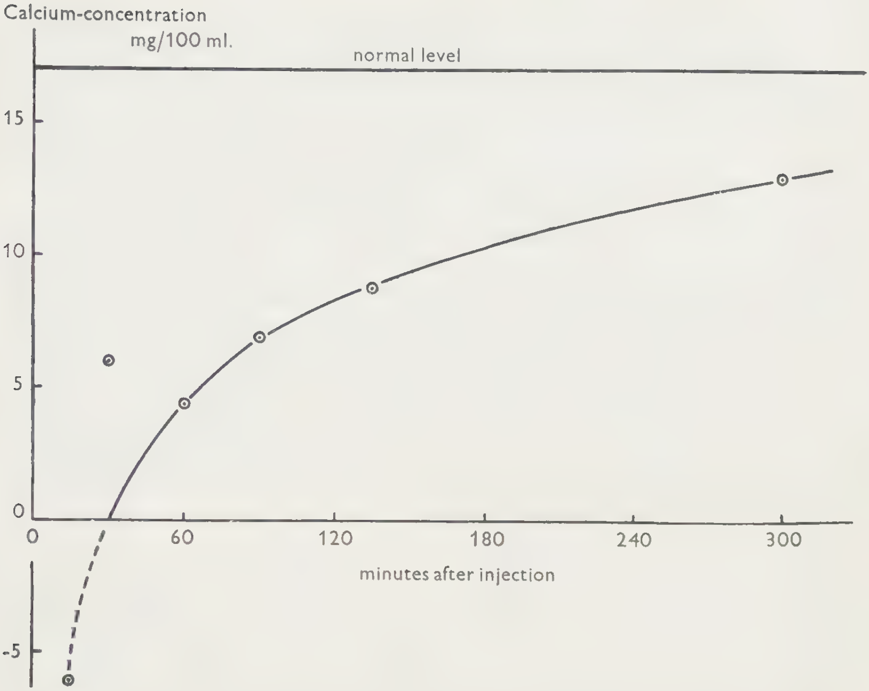

Fig. 3. Calcium concentration after injection of ethylenediamine tetraacetate.

molymph. We showed, however, that even the injection of rather large amounts of distilled water (80 μl) could not bring about a decrease of more than about 30 per cent. We therefore carried out a number of experiments, in which 30 μl of a 67 mMol. ethylenediamine tetraacetate solution was injected. This amount would be sufficient to chelate all the calcium and magnesium present in the haemolymph of the insect, at least if simple mixing occurred. From the results the following conclusions could be drawn:

a. Immediately after the injection, (determinations made after 15 min.) no free calcium was present in the thoracal or in the abdominal haemolymph.

b. In the following five hours there was a steady increase of the calcium concentrations, but complete recovery did not occur in this period (see fig. 3). After 5 hours approximately 75 per cent of the normal concentration was found. No calcium or magnesium determinations were made after more than 5 hours.

c. The same may apply to magnesium, but here the results did not allow of a quantitative interpretation.

d. The insects were seriously affected by the injection. The symptoms of intoxication (paralysis, slow movements, the animals lying on their backs) appear mostly within 15 minutes and last for several hours. About 30 per cent of the insects die within 24 hours, the others recover completely.

6. INJECTION OF AND EXPOSURE TO GAMMA BENZENEHEXACHLORIDE

As in our laboratory a study is undertaken of the mode of action of gamma benzenehexachloride (gamma BHC), we were especially interested in the effects caused by gamma BHC intoxication. Injection of large doses of gamma BHC resulting in very severe symptoms, did not alter significantly the concentrations of sodium, chloride, total nitrogen or non-protein nitrogen. Cockroaches exposed to concentrated deposits of gamma BHC causing marked symptoms, showed quite normal calcium and magnesium values. Moreover, the ability to restore nearly normal calcium concentrations after injection of concentrated calcium chloride solutions was unimpaired.

IV. GENERAL DISCUSSION

In the second section of this paper we stated that the variability of the concentrations found for the mineral constituents in the haemolymph of *Periplaneta americana* was rather small. In the third section we were able to show that the insects had a marked ability to restore normal concentrations after severe disturbances. Moreover, in most cases the insects showed a high tolerance. We should like to stress the possibility that this high tolerance could be to some extent a consequence of the strong regulating ability.

Furthermore it is very important to note that (with one exception – ethylenediamine tetraacetate) injection of large amounts of fluid into the abdomen never caused large changes of the concentrations in the thoracal haemolymph. This possibly can be partly explained by the slow circulation of haemolymph through the body. The small rate of circulation might give the insects an opportunity for regulation before the "disturbance" reaches the thoracal and head parts of the body.

The results of our experiments on regulation point to a transfer of ions rather than to a transfer of water. Removal of ions from the haemolymph might be accomplished by the Malpighian tubes, but no experiments were performed to investigate this point.

V. SUMMARY

The paper deals with the chemical composition of the haemolymph in the insect *Periplaneta americana*.

The first section gives a description of the experimental techniques.

Special attention is given to the method for the determination of calcium in small amounts of haemolymph. Microtitration with ethylenediamine tetraacetate using a well known Linderstrom-Lang technique gave very reliable results (see Table I). The methods for the determination of sodium, potassium, chloride, total nitrogen, non-protein nitrogen, and total reducing value are only briefly described, as they are principally similar to those used in human clinical chemistry. Descriptions are also given of the techniques for injection, and for collection of haemolymph.

The second section deals with the composition of normal haemolymph. A large number of determinations of Na, Cl, Ca, Mg, T.N., N.P.N., and T.R.V. in individual insects were performed to gain a better insight in the individual and sexual differences. Moreover a large number of determinations in pooled haemolymph were performed. The results are summarized in Table II.

The values obtained are compared with those found in literature and discussed.

The third section describes several kinds of experiments to test the regulatory power and the tolerance of the insects. Varying amounts of distilled water or salt solutions were injected and concentrations determined after different intervals of time. It is shown that the insects are able to restore normal concentrations rather rapidly. This especially applies to the results obtained after injection of very concentrated solutions of calcium chloride, magnesium sulphate and ethylenediamine tetraacetate (see figs. 1, 2, and 3). The tolerance proved to be very high if compared with that in mammals. No abnormalities in the behaviour of the insects resulted from the injection of 30 or 60 μl of solutions containing 200 mg calcium or 300 mg magnesium per 100 ml. The injection of large quantities of potassium or ethylenediamine tetraacetate sometimes caused paralysis and death.

By comparing the concentrations found in abdominal haemolymph and thoracal haemolymph after intra-abdominal injection of a concentrated calcium chloride solution an estimate of the time necessary for complete mixing of the haemolymph could be made. It proved to be in the order of 30–60 minutes.

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It is a very great pleasure for us to thank Dr. C. A. PARKER, Poole, Great Britain, for his thorough correction of the English text.

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ANNUAL REPORT
OF THE ZOOLOGICAL STATION OF THE NETHERLANDS ZOOLOGICAL SOCIETY
FOR THE YEAR 1954

In the previous report it was stated that of late years a gradual change has been noticeable in our research. In the zoological work emphasis has shifted to problems of details and at the same time attention has become focused more and more on behaviour and physiology. This state of things implies that outdoor work, which would yield general results, was promoted to a less degree, whereas greater facilities were made available for experimental work on various subjects. However, as students often favour outdoor research, this kind of work is continued, which is gratifying because it frequently contributes to opening up new lines of enquiry.

The investigation on the spatfall of the mussel (*Mytilus edulis*), which has been in progress for several years, was now taken up by Mr. REDDINGIUS (Leiden). His observations were a continuation of those made by Mr. BAS in 1953, which aimed at estimating the role of transport along the tidal flats among small mussels that have passed primary settlement. The minute size of the youngest spat requires microscopic examination for counting and measuring. This takes so much time that a single person is seriously hampered in extending his observations to any considerable scale. It would therefore be more efficient to have three men engaged upon this work at the same time rather than in succession. Nevertheless, our insight into the matter has gradually increased and we are looking forward to the publication of Mr. REDDINGIUS' results, together with those obtained by Mr. BAS in 1952 and 1953, and perhaps with those of others. Mr. DRINKWAARD (Utrecht) studied the settling of the mussel in the field as well as in the laboratory. Flower-pots were mounted on iron bars to serve as a substratum at different levels in the water. The results were disappointing because of the small numbers of individuals that actually attached themselves to the pots.

In the laboratory Mr. DRINKWAARD examined the influence of light on the settling of young mussels. In spite of their preference for illumination the animals seem to prefer and settle on dark substrata rather than light ones. The results are still in a preliminary stage and the work should be continued.

Some progress was also made in another part of lamellibranch research, which deals with the difference in behaviour between younger and older planktonic larvae of bottomdwelling species. In 1950 Mr. LUCAS studied the subject and after him Mr. ANTHEUNISSE in 1952. Generally, pelagic larvae of benthic animals are kept in the upper water layers by their need of light, but when reaching the stage of metamorphosis, they are forced to go down to deeper levels so that their reaction to light must become different by this time. THORSON, however, put forward the supposition that benthic animals of shallow waters maintain the same reaction to light throughout their larval life. An attempt was made to test this supposition for the larvae of *Littorina littorea*. The work was carried out by Dr. AL KHOLY from the Marine Biological Laboratory at Ghardaqa (Red Sea, Egypt) during his six months' stay at Den Helder in 1954. Relative frequencies of younger and older larvae were evaluated at different depths during slack high water at midnight and at noon. Behaviour towards light was found to change during larval life in such a way that the need of light becomes stronger in the older stages. The results will be published in "Archives Néerlandaises de Zoologie".

The previous annual report included a discussion of the work of Miss BLOKZIJL (Groningen), who demonstrated that lamellibranchs will produce more pseudofaeces and fewer faeces in waters carrying a greater amount of particulate matter. This means that more food is rejected in waters with a greater silt content. Mr. KRISTENSEN, assisted by Mr. DRAL, attempted to study the influence of suspended matter on the uptake of food in a different way by determining growth in waters with different silt content. These experiments formed part of a more comprehensive series which was planned to find out to what extent growth and mortality in *Cardium*, *Mya*, and *Mytilus* depend on such environmental factors as absence of light, quantity of suspended matter, and salinity. These experiments have not, however, yielded conclusive results as yet.

In 1954 Miss HEIKENS (Groningen) finished her item of research initiated at Den Helder in 1950. With the assistance of Mr. DRAL she determined the quantities of water pumped by mussels at various temperatures. Her method depended on the fact, ascertained by TAMMES and DRAL, that mussels retain all particles of a size of about 40 μ. The rate of pumping was calculated from the decrease in concentration of a suspension of spores of *Lycopodium*. The data revealed that mussels continue pumping till the temperature is lowered to about zero, but the quantity pumped becomes extremely small then. This was a confirmation of earlier indications from other data.

In connection with this investigation Mr. DRAL studied the influence of temperature on the mussel's pumping activity by a method described by WALLENGREN (1905). A light pendulum, carrying a minute mirror, is suspended in front of the exhalation siphon so that the strength of the watercurrent can be measured from the deviation of a beam of light reflected by the mirror. These observations revealed a more or less linear relation between the temperature and the quantity of water pumped within the temperature range of – 0.5 to 9.-° C. Even at – 0.5° C. pumping is not altogether stopped. In the common oyster pumping is known to stop at about 5° C.

As was reported last year, Mr. GLAS (Groningen) studied the response of the common shrimp (*Crangon crangon*) to a diminishing head of water. This work was now continued and extended by Mr. HEYLIGERS (Utrecht), who arrived at the conclusion that during the day the shrimps perceive the fall of the surface with their eyes, without the help of antennae; whereas at night they probably observe changes in height when swimming. The water depth preferred when hiding is different in individuals of different size: the larger animals tend to prefer a greater head of water than the smaller ones.

Mr. HAECK (Utrecht) also took up an item which had been studied before at Den Helder, without its having yielded conclusive results so far. In 1950 Mr. WILLEMSEN had tried to demonstrate the shrimp's perception of minute variations in salinity. He endeavoured to condition the shrimps, as BULL had successfully done with fishes. The experiments had miscarried because of the shrimp's readiness to become conditioned to adventitious factors rather than to salinity. At first Mr. HAECK had to cope with the same difficulty, but after some time he gained evidence that shrimps do probably perceive variations down to 0.20 $^0/_{00}$ Cl′. Since the threshold had not yet been reached Mr. HAECK will carry on his experiment in 1955. Up to now, little was known as to the threshold of perception of salinity changes in evertebrates; SPIEGEL believed that *Crangon* could perceive NaCl changes of about 2 $^0/_{00}$.

Another piece of research, started by Mr. ROESSINGH (Leiden) at Den Helder and Plymouth in post war years, was taken up by Mr. LEEUWENBERG (Utrecht). It dealt with the influence of external factors on the tendency of *Psammechinus miliaris* to cover itself with foreign substances. The habit was found to be most apparent in full daylight, and less so in faint light. When the animals are given small pebbles, shells etc., they will completely cover themselves within half an hour, using their tube-feet for getting hold of the rubbish. LINDAHL and

J. Runnström found that animals from deeper water, which are less pigmented, are sooner inclined to cover themselves than animals from shallow water. They supposed that Lichtschutz might be the ultimate aim. Predators, such as the lobster (*Homarus*) and the edible crab (*Cancer*) will, no doubt, find *Psammechinus* by scent or taste, and not by vision, so that the disguise will be useless against these enemies at least.

Some interesting observations on the cockle (*Cardium*) were made by Mr. Roosenschoon (Utrecht). They concerned the way in which *Cardium* digs itself into the sand and contributed to the study of animal behaviour. He endeavoured to analyse the digging activity, and it seems likely that the chain of actions can be set off even when the cockles hang freely in the water without any contact with the bottom. The observations might stimulate further ethological work.

The study of nudibranch slugs, which had been in progress during former years, was suspended, except for the work of Mr. Stock (Amsterdam), who wanted to get acquainted with the methods for his intended investigation at Roscoff, and of Mr. De Wolf (Amsterdam), who tried to continue last year's work. Both attempts (of 19 and 12 days respectively) were hampered by the difficulty of obtaining sufficient numbers of slugs.

The investigations of Mr. De Blok on the influence of lunar and tidal periodicities on the reproduction of marine animals was continued. The work is financed by the Netherlands Organization for Pure Research. Its progress is slow but sure. A theoretical treatise was composed, from which it appears likely that various factors are instrumental in inducing reproductive rhythms in the sea. In cooperation with Mr. Duk, instrumentmaker at the Zoological Laboratory at Leiden, an apparatus was designed for separately testing the action of each of the factors that will accompany tidal and lunar phases. The costs are estimated at *f* 21 300.—, an amount that has also been granted by the Organization. The investigation is supervised by Mr. Korringa (Bergen-op-Zoom) and Mr. Verwey.

The data obtained this year by Mr. Kristensen, by buying up specimens from fishermen, are again tabulated. Contrary to the findings of 1953, the southern species were scarce, whereas the occurrence of northern species was normal. Southern species, viz. the cuckoo gurnard (*Trigla cuculus*), the black bream (*Spondyliosoma cantharus*), the hake (*Merluccius merluccius*), the dory (*Zeus faber*), the pilchard (*Clupea pilchardus*) and the cephalopods *Loligo vulgaris* and *Octopus vulgaris* were less numerous than in former years. Only the rays *Raia brachyura* and *R. montagui* were rather common. Mr. Kristensen holds the opinion, that this year's scarcity of the southern species was brought about by the low spring temperatures, which must have checked their northward migration. The northern species did not respond to the low temperatures and appeared in normal numbers. In this respect there was a marked difference with 1953, when the northern species did migrate farther south. As in 1953, the haddock (*Gadus aeglefinus*) predominated among the northern species and considerable numbers were again found off Den Helder in Texel Hole.

In the spring of 1954 the high salinity of the Wadden sea was conspicuous, which, no doubt, made great numbers of *Sepia* and *Loligo* spawn in the Wadden area. It is not clear whether this high salinity also caused the abundance of young cod (*Gadus callarias*) and sole (*Solea solea*) (born in 1954) and the scarcity of young (1954 born) whiting (*G. merlangus*) and plaice (*Pleuronectes platessa*). Rather, it seems likely that the abundance or scarcity of these animals in the Wadden sea depends directly on the greater or smaller success of their spawning in the southern North Sea. The great numbers of young cod would then be due to the low temperature in February; low temperatures may be considered favourable for this species.

During the frost period of February Mr. KRISTENSEN made some observations on the tidal flats. Between the ice and the frozen bottom he found water rich in H_2S and poor in oxygen. Salinity had reached twice the normal value as a result of freezing. In this medium mussels, cockles, clams (*Mya arenaria*) and polychaetous worms died in great numbers, whereas gastropods, viz. *Littorina* and *Hydrobia*, survived.

In the water the most extreme salinity value was twice higher than normal, namely 32.20 $^0/_{00}$ Cl′ at a temperature of -2.9^0 C. In the bottom even lower temperatures were measured, viz. -5.9^0 C. This means, that in preceding days the watertemperature must at least have been equally low. In this connection Mr. POSTMA draws attention to RINGER's work of 1906. RINGER pointed out that the water can only reach such a low temperature when freezing has increased the salinity to 50 $^0/_{00}$ Cl′, which is about three times the normal value. The observation is also important because RINGER has demonstrated that at these low temperatures calcium carbonate is precipitated. So under these extreme conditions lime could be formed on the tidal flats by an inorganic process.

During the frost period considerable mortality of the molluscs *Gari fervensis*, *Dosinia exoleta* and *Cardium norvegicum* occurred in the southern North Sea. Mr. KRISTENSEN believes these species extend their area of distribution into the North Sea during periods of higher temperature, but perish again during extreme cold.

Our hydrographic research derived considerable advantage in 1954 from a visit of Prof. KREY of the Institut für Meereskunde at Kiel, who worked six weeks at the Zoological Station at Den Helder in return for a stay made by Mr. POSTMA at Kiel in May and June. This exchange

Species	Sex; Size (cm)	Locality (ST Means buoy on the Silverpit-Texel route)
Southern migrants, supposed to have entered the North Sea through Dover Strait		
Scyliorhinus stellaris	♀ 54; ♀ 56; ?; ♀ 41	Texel Hole; ST 4; ST 3; Texel Hole
Raia brachyura	38–107	1 spec. off Petten 12 m (28 Aug.); Texel Hole-Tea Kettle Hole-Oyster Grounds
Raia montagui	29–67	ibidem (42 spec. in one catch in Tea Kettle Hole)
Raia undulatus	♂ 57	Tea Kettle Hole
Raia naevus	♂ 62; 70	N. of Terschelling 31 m.; ST 3
Clupea pilchardus	adults	May: Texel Hole; Aug.–Sept.: 1 spec. Zuiderhaaks 5 m, others from Wadden Sea
Merluccius merluccius	♂ 54	NW. of Texel, 38 m
Spondyliosoma cantharus	25; 32; ♂ 26; 13; 28	from off Egmond 27 m to N. of Terschelling 36 m and ST 4
Atherina presbyter	9; 9; 16; 8; 9; 9	May: off Callantsoog 4 m. Aug.: many adults and newly born from brackish waters on Texel
Trigla cuculus		mostly from Texel Hole area
Trigla lineata	♂ 29	between ST 4 – ST 5
Northern fishes, likely to have entered the southern North Sea from the North		
Gadus virens	21	Petten 5,5 m
Molva molva	40; ♂ 55; 49	ST 3; NW of Terschelling 36 m; NW of Texel 29 m
Onos cimbrius	25; 22; 19; 19; 11; 9	Texel Hole; off IJmuiden 29 m; Texel Hole (2 spec.); Petten 4 m; Texel 4 m
Anarhichas lupus	40; 35	Tea Kettle Hole; Texel Hole
Hippoglossus hippoglossus	♀ 54	ST 4
Fishes, whose direction of migration is uncertain		
Raniceps raninus	11; 6; 10; 6; 7; ± 10	coastal water between Petten and Texel 4–11 m
Labrus berggylta	25–35	from off IJmuiden to ST 4
Ctenolabrus rupestris	7	Malzwin (Wadden Sea)
Spinachia spinachia	15	off Petten 5,5 m
Scorpaena dactyloptera	21; 14	ST 4; off IJmuiden 29 m
Evertebrates, "rare" in the area off Den Helder		
Portunus puber		Texel Hole
Nephrops norvegicus		Texel Hole – ST 4
Illex illecebrosus	♀ 26.5	Texel Hole
Todaropsis eblanae	10	Texel Hole
Loligo vulgaris		mostly from coastal waters (no data collected June–Oct.)
Loligo forbesi		mostly from Texel Hole Area (no data collected June–Oct.)
Sepia officinalis		mostly from coastal waters and Wadden Sea
Eledone cirrhosa	7.5–11.5	off Petten 5 m – Botney Gut 50 m
Scaphander lignarius		ST 1 – ST 2

Numbers per month											
J	F	M	A	M	J	J	A	S	O	N	D
			2	—	—	—	—	—	—	1	1
			3	—	2	—	1	—	1	1	5
7	—	49	23	5	—	1	1	—	2	7	53
						–					—
					1	—	—	—	—	—	1
				4	—	—	16	2			—
				–	1	–					
						—	4	—	—	—	1
				6	—	—	∝				–
				5	17	7	—	1	—	—	1
											—
			1								
2	—	—	—	—	—	1					—
1	—	1	4								—
—	—	1	1	—	—	—	—	–			—
				1	—	—	—	—			—
—	—	2	3	—	—	—	—	1			—
—	—	3	1							—	—
				1							—
			1								
1	—	1	—	—	—	–					—
–	—	—	—	—	—	—	—	—	—	—	1
1	1	2	—	1	2	1	—	—	1	—	1
—		–	–	1							—
										1	—
—	—		7	248	?	?	?	?	?	—	1
29	—	—	—	—	?	?	?	?	?	32	118
6	—	—	—	50	48	12	37	8	10	1	4
—	—	3	3	—	—				—	—	—
–	—	—		—	–	–	1		—	—	—

was promoted by financial aid on the German side and from the Organization for Pure Research. In close cooperation with Mr. POSTMA Prof. KREY examined the composition of suspended organic matter in the Wadden Sea. The chlorophyll content of live phytoplankton was compared with that in detritus. An exact knowledge of this relation is essential in evaluating the fertility of water masses. A closer analysis of the relation between dead and living matter was made possible by a specific test for live protein, which had been developed by Prof. KREY. These determinations were carried out together with those for nitrogen, phosphor, etc.

Prof. KREY and Mr. POSTMA continued their cooperation in May during a visit of the latter to Kiel. On this occasion several watersamples from the Baltic Sea were analysed and attention was again focused on the relation between living and dead matter. They had an opportunity to compare two methods for determining organic phosphorus. The results justified every confidence in the method employed.

Subsequent to his visit to Kiel, Mr. POSTMA became acquainted with the Hydrobiological Institute at Plön and then spent a fortnight at the German Hydrographic Institute at Hamburg. Here, in cooperation with Prof. KALLE, he carried out an investigation into the origin of a turbidity maximum in the lower Elbe. A similar maximum is found in almost every river estuary in Europe and in many cases, notably in the Elbe, it has been ascribed to flocculation of the colloids of the river water by the minerals of the sea. It was shown by this investigation, in which samples of river water were treated with sea water, that no such flocculation takes place in the Elbe, at least not on a scale sufficient to explain the existence of the turbidity maximum. Mr. POSTMA assumes that hydrographic factors are the main causes of this turbidity. Recently, Ir. SANTEMA of the Rijkswaterstaat arrived at the same conclusion in regard to the lower Rhine.

Mr. AL KHOLY also cooperated with Mr. POSTMA, and further Mr. RD. ENGKOES SOERIAATMADJA, analyst of the marine biological laboratory at Djakarta (Java), joined the hydrographic team. Mr. AL KHOLY also tested the stability of chlorophyll in a dead culture, which is of interest in connection with the occurrence of chlorophyll in non-living organic matter in the sea. Perhaps a short contribution on the subject will appear in print.

Mr. SOERIAATMADJA studied the methods of hydrographic work, but at the same time furnished a contribution to our own line of research. He analysed the composition of the water in the North Holland Canal and traced the influence of this water in the Wadden Sea near Den Helder. Since salt water is a nuisance in the low lands of the region, fresh water is let in near Amsterdam from the Yssel Lake and drained off at Den Helder. This management tends to get rid of the salt water penetrating the sluices. The water of the canal contains considerable quantities of phosphate and nitrate, which fertilize the tidal waters nearby. The observations were made in November and December and will be continued after the departure of Mr. SOERIAATMADJA.

A hydrographic survey of the Eems and the Dollart was carried out in cooperation with the Royal Netherlands Meteorological Institute (K.N.M.I.), the Oceanographic Section of which has taken water samples from a point near Embden down to the sea. A comparison with the western part of the Wadden Sea revealed an interesting difference. The samples from the Dollart contained much more suspended matter (living and non-living) than those from the western part of the Wadden Sea, and the Dollart-water was therefore more nutritive. Both Dollart and western area act as a store for suspended material, but the river Eems, contrary to the river Yssel, considerably adds to the fertility of these waters.

The Government Institute of Fisheries Research applied to the Station for assistance in finding out whether the densely inhabited mussel grounds off Den Oever (Wieringen) cause a local decrease in the quantity of suspended matter, organic as well as inorganic. The investigation was undertaken jointly by Mr. HAVINGA, Mr. KORRINGA, and Mr. POSTMA. In particular the chlorophyll content was taken as a measure for the amount of organic matter. The chemical analyses were carried out at Den Helder by Mr. KORRINGA and the personnel of the Zoological Station. In connection with this work cruises were made in the western part of the Wadden Sea. The work did not yield conclusive results and will probably be continued later on. The data obtained so far contribute, however, to our knowledge of the occurrence of chlorophyll, the distribution of which has had Mr. POSTMA's attention for several years.

Assistance was also offered to Mr. KORRINGA in his effort to estimate the productivity of the Easter Scheldt. A considerable number of phosphorus determinations were made on water samples collected at regular intervals on Ierseke Bank and more accidentally in other locations.

In April and August further aid was given to an investigation initiated by Rijkswaterstaat, section Hoorn, on the transport of silt in Den Helder harbour. In former reports the changes that have here taken place were mentioned. The silting up of the new harbour exceeds expected standards and Waterstaat has therefore tried to gain an insight into the settling of the sediments. The Zoological Station determined the silt content of a thousand water samples. In an attempt to limit sedimentation in the new harbour, the old outer harbour (the so-called Nieuwe Diep) will now also be dammed off in its outer part.

In the Nieuwe Diep salinity and temperature determinations were carried out daily. This routine work was supplemented by a number of oxygen determinations. In front of the Zoological Station the water is high in salinity near the bottom, most of the time even higher than at high tide formerly when the currents could pass freely. The deeper water is therefore quite suitable for the aquaria, but in summer its oxygen content is poor. During the last few years the water has therefore been pumped up from the Nieuwe Diep during winter only, whereas a waterboat maintained the supply from the Marsdiep in summer. The management has been satisfactory so far, but future arrangements are uncertain as long as the construction of the new harbour has not been completed.

Besides the persons already mentioned. Mr. J. A. W. LUCAS (Leiden), Mr. R. PEELEN (Amsterdam) and Mr. J. JANSONIUS, a geologist from Utrecht, spent short terms at Den Helder, mainly for orientation. Further Mr. POSTMES (Utrecht) and Mr. VAN DER HEIDE (Amsterdam) spent one day at the Station for fixation of specimens, while Dr. J. S. ZANEVELD (Leiden) had a five days' stay to get acquainted with methods of aquarium management and research methods in connection with the erection of a marine biological laboratory on Curaçao (Caribbean).

The number of students attending the Station's summer courses amounted to 29 this year; 20 of them were from Leiden, 8 from Utrecht and 1 from Amsterdam. The courses were jointly given by the five members of the staff, including Mr. DE BLOK, from June 21st to July 3rd and from July 5th to July 17th.

Apart from this, Mr. VAN NIEUWENHOVEN and Mr. KOOY, assistants at the Physiological Laboratory of the University of Amsterdam, gave a physiological course, which had been planned together with Dr. J. DE WILDE. From June 9th to June 16th 12 students attended this course.

The total number of man-days for individual workers and summer course participants in 1954 amounted to about 1550. In the previous report it was explained that this number varies a good deal in the course of time; over the period 1947–1954 it averages about 1080.

Considerable expenditure was again laid out for the maintenance of the building and the students' lodge, which were both painted this year. The caretaker's sitting-room was given a better appearance. The electric circuits near the aquaria were replaced by waterproof cables and finally a dark room for photographic work was added to the building.

The Mekog Ltd. transferred to us the new aquarium, including plastic pipings and pumping installation, for *f* 18500.—. This amount was furnished from a fund accumulated from payments by

Mekog Ltd. for the contracted research on industrial waste waters, carried out by Dr. TAMMES in previous years. The Bleeker electric spectrophotometer that had been in use for the same purpose was taken over by us for ƒ 2 500. —. The aquarium and the photometer are most valuable acquisitions for the Station.

The Station's equipment was further supplemented by additional instruments, for which the Government furnished an extra grant of ƒ 5 000.—. The purchases included a Christ centrifuge of 1 litre capacity. In general, the Station's equipment has been much improved of late years. This was especially noticeable in 1954, thanks to the above mentioned extra grant and the raising of the regular allocation for instruments to ƒ 3 600.—.

The Station's vessel "Max Weber" did not require heavy expenses. The ship was in fairly regular use, also during the winter. It passed a general inspection by Scheepvaartinspectie which did not lead to large expenditure. The Station obtained the use of a second rowing-boat, which is the property of the Organization for Pure Research and had been used by the Foundation for Marine Geology at Groningen. A second rowing-boat will often be an advantage for work on the tidal flats.

There were no changes in the personnel, except for the departure of the student-analyst G. VAN DER WAL, who left the Station on October 1st. A memorable event was the conferment of the doctor's degree on Mr. POSTMA. His stay at Kiel and Hamburg has already been mentioned. In October and November Mr. POSTMA worked at the Zoological Station at Naples. His program had been set up in cooperation with Mr. KORRINGA, who had visited Naples in spring. Their aim was to study the fertility of some small lagoons which communicate with the Mediterranean. Attention was also given to the fertility of the Gulf of Naples. The latter observations will perhaps contribute to a better understanding of fertility relations in the Mediterranean in general. During his stay in Italy Mr. POSTMA also attended the Congress of the "Union Géodésique et Géophysique Internationale", which was held at Rome from September 14th to October 1st.

The condition of the library was quite satisfactory, thanks to the good care of Mr. WESTENBERG and Miss STOLL. The main feature was an extension of our exchange program. Special efforts were made to acquire large sets of periodicals at once in exchange for backnumbers. The number of exchange relations now amounts to about 225. The library is becoming more and more cramped for space and an expansion is urgently necessary. Only a few books were obtained by purchase and quite a lot of reprints by donation, for which we express our sincere gratitude. VON BUDDENBROCK's "Vergleichende Physiologie" was received as a present from Prof. KREY, Kiel.

The supply of study material to laboratories, schools, zoological gardens, private workers and amateurs brought in *f* 4 392.08. The purchase of animal specimens required a sum of *f* 3 375.33 and expenditure for wicker-bottles, preserving solutions, packing, freight etc. was *f* 641.94, from which *f* 110.33 was returned; this resulted in a nett profit of *f* 485.14. This side of the Station's activity takes much time and is therefore costly, but at the same time important. The business could be made selfsupporting by charging for the salary costs, but this would raise the prices considerably.

The Government grant for 1954 amounted to *f* 87 700.—, of which *f* 66 000.— was allocated for salaries and national insurance, which left *f* 21 500.— to defray further expenses. *f* 5 000.— of this sum was especially destined for some expensive instruments, so that *f* 16 500.— remained at our disposal for running the Station.

Den Helder, March 1955
J. Verwey

THE PREFERENCE
OF LITTORINA OBTUSATA FOR FUCACEAE

by

A. VAN DONGEN
(*Zoological Station, Den Helder*)

I. INTRODUCTION

In an earlier paper in this journal BARKMAN (1955) discussed the causes of the horizontal and vertical distribution of the tidezone snail *Littorina obtusata.* This species is tied down to the tidal zone through an innate negative geotaxis, which keeps it away from deeper water, and a dislike for strong light and desiccation, which prevents its negative geotaxis from carrying it to too high a level. It is further chemotactically attracted by the Fucaceae upon which it lives. The species is subdivided into a number of varieties. Of these variety *citrina* is found especially in the lower half of the tidal zone, whereas variety *olivacea* is chiefly found in the upper half. Broadly speaking, they are therefore found on different Fucaceae. BARKMAN tried to ascertain whether the different distribution of the two varieties in nature was caused, apart from a different reaction to abiotic factors (gravity, light, wave action), also by differences in their preference for algae, and he came to the conclusion that the preference for Fucaceae is more pronounced in variety *olivacea* than in variety *citrina* (which is more often than *olivacea* found on *Chondrus crispus*) and that within the group of Fucaceae variety *citrina* clearly has a preference for *F. serratus*, whereas the results in regard to *olivacea* were doubtful; BARKMAN was inclined to suppose, however, that its preference within the Fucaceae differed from that of *olivacea.* In connection with these observations it seemed worth while to find out whether the two above mentioned varieties would react differently to the scent emitted by the different species of Fucaceae and a number of experiments were undertaken accordingly. The work was carried out in the months of August and September 1953 at the Zoological Station, Den Helder. I owe many thanks to the director, DR. J. VERWEY, for his suggestions and his help in preparing this paper, to DR. J. WESTENBERG, for his aid in its statistical part, to Mr. J. A. A. SPIEKERMAN, Den Helder, for the correction of the English text.

II. MATERIAL AND TECHNIQUE

The experiments were carried out in the same way as VERWEY's experiments described in BARKMAN's paper.

Sea water was kept flowing over the bottom of a shallow concrete aquarium tank of 250 × 67 × 15 cm (fig. 1). The water level in it was kept very low, 1 cm or less, in order to keep the snails with their strong negative geotaxis from climbing the walls. The snails were placed at the downstream end of the tank and a few pieces[1] taken from the fronds of Fucaceae were laid at the upstream end between two bricks, which formed a passage of 10 cm width for the incoming water. The distance between the snails and the algae was first 2 m, in the definite experiments 1 m; the distance between the snails and the water outlet was also 1 m. The experiments with algae alternated with blanks. Each experiment lasted 12 hours. In between experiments the snails were regularly fed algae at the starting place. After each experiment the tank bottom was thoroughly cleaned to make sure that algal scent would not interfere with the controls. After the snails had been used a few times the animals were replaced by others.

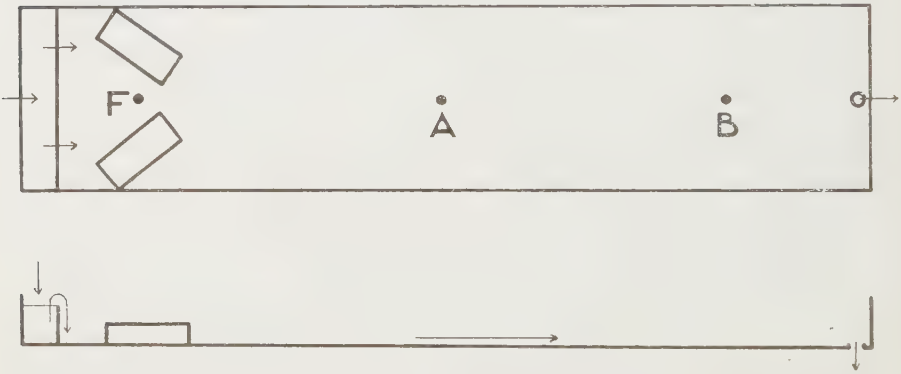

Fig. 1. Scheme of experiments. A and B: centres of places where snails were deposited. F: centre of place where Fucaceae were deposited. Arrows denote direction of water current. For further explanation see text.

The first experiments were carried out in the dark, so that light influence should not interfere. Since the number of snails leaving the starting place remained very low, a total illumination of 20 Watt was provided in the form of 4 Philips bulbs of 5 Watt, 80 cm above the tank bottom and regularly spaced over the tank. Also with this weak illumination the animals remained rather inactive. Therefore, the illumination was made stronger and 4 bulbs of 60 Watt were installed instead. The snails were much more active now and the definite experiments were therefore carried out under this illumination.

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[1] Only in the experiments carried out *in the dark* more than a few (even a great many) pieces were used.

In a second series of experiments the reaction of the snails was studied under different conditions. Barkman had already adopted the same method. The 4 species of Fucaceae were laid out in a circle, with the snails in the centre. The distance between the snails and the algae was about 15 cm. After 12 hours the numbers of snails found on each of the Fucaceae were counted and the animals were deposited again in the centre after the circle of algae had been turned 90°. The experiment was carried out 4 times, so that each algal species had taken the place of the others once. The illumination in this case was provided by a 60 Watt-bulb, hanging right above the centre at a height of about 80 cm.

III. RESULTS

I. PERCEPTION OF FUCACEAE FROM A DISTANCE

A. Experiments in the dark

In the first of the experiments carried out in the dark the snails were placed at a distance of 200 cm from the water inflow. The results after 12 hours are given in table I.

TABLE I

Upstream movements of *Littorina obtusata* in the absence and presence of Fucaceae. Algae at 200 cm distance. Complete darkness.

	No algae at inflow		*Fucus spiralis* at inflow		*Fucus vesiculosus* at inflow	
	Total	Upstream	Total	Upstream	Total	Upstream
variety *citrina*	94	19				
	94	31				
	188	50	120	57	118	36
		(27 %)		(47 %)		(30 %)
variety *olivacea*	31	5				
	74	22				
	105	27	71	44	67	35
		(26 %)		(62 %)		(52 %)

The results indicate that the scent of *Fucus*, especially in the case of *F. spiralis* (perhaps less so in the case of *F. vesiculosus*) has some influence on the snail when produced at a distance of 200 cm. Of the upstream animals very few, however, reached halfway the distance to the water inflow. In the experiment without algae there were 2, in that with *F. spiralis* 4, in the case of *F. vesiculosus* again 2. No snails reached *Fucus* or its close proximity. It is doubtful whether the variety *citrina* behaved differently from the variety *olivacea*.

Because the distance of 200 cm might have been too great, the experiments were repeated with a distance between the snails and the water inlet of 100 instead of 200 cm. The experiments were carried out with *Fucus serratus*. Three out of 98 animals now reached the neighbourhood of *Fucus*, 27 reached the part of the tank between 50 and 100 cm upstream, the others were found in the downstream part including the first 50 cm upstream. In view of the many branches of *Fucus* used this result was considered insufficient as a basis for further experiments and the distance between the snails and *Fucus* was further decreased in subsequent experiments. It was quite clear, however, that the outcome of the experiments with a distance between snails and *Fucus* of 100 cm was much "better" than that with a distance of 200 cm. Apparently, a difference of 100 cm was rather much for the animals.

In the experiments following next the distance between the snails and the water inlet was again made shorter: now 66 and 33 cm. Even in these cases, however, the number of snails reaching *Fucus serratus* was only small, in spite of the fact that many branches of *Fucus* were used. Since VERWEY had found that even small pieces of *Fucus* attracted the snails from 150 cm distance we wondered whether the constant darkness could have something to do with the results and accordingly started experiments with a weak illumination. VERWEY had made his experiments in daylight and night conditions, but during the night there was always a faint illumination.

B. Experiments under a weak illumination

In the experiments which followed now 4 bulbs of 5 Watt each were used, providing a total illumination of 20 Watt. The snails were deposited at 100 cm from the water inlet and after 12 hours their distribution was examined. In these and later experiments the distances covered by the snails were classified in 3 groups:

Group 1, including the downstream part of the tank and 50 cm of the upstream part;
Group 2, between 50 and 100 cm upstream;
Group 3, more than 100 cm upstream, on and around *Fucus*.

The results of these experiments, which were again carried out with *Fucus serratus*, are given in table II.

TABLE II

Movements of *Littorina obtusata* in the absence and presence of *Fucus serratus*. Algae (few pieces) 100 cm distant. Total illumination 20 Watt.

	Variety *citrina*			Variety *olivacea*		
Group	1	2	3	1	2	3
No algae at inflow	120 98.4%	2 1.6	0 0	58 92.1	5 7.–	1 0.9
Fucus serratus at inflow	105 92%	8 7.–	1 1	56 87.5	6 9.4	2 3.1

Though in these experiments the percentage of snails reaching the algae was still very low it was apparent that the animals were somewhat more mobile than in the experiments carried out in complete darkness. It was therefore concluded that the illumination should be stronger.

The experiments indicate that the scent of *Fucus serratus* has some influence on the snail when produced at a distance of 100 cm. It is doubtful whether variety *citrina* behaves differently from variety *olivacea*.

C. Experiments with an illumination of 240 Watt

Experiments were now carried out with an illumination of 4 bulbs of 60 Watt each. The snails were much more active now and the influence of the algae became measurable, as in the earlier experiments of VERWEY. The movements were registered in the same way as under B. The total number of experiments amounted to 25; 5 of them were carried out without algae at the water inflow, 5 with each of the 4 species of Fucaceae found at Den Helder. The results are presented in table III.

It should be added that the 4 species of Fucaceae are given here in the order in which they inhabit different levels of the tidal zone, *F. spiralis* growing highest, *Fucus serratus* lowest. It has already been stated that variety *olivacea* of the snail is especially found in the upper half of the tidal zone, variety *citrina* in the lower half.

TABLE III

Movements of *Littorina obtusata* in the absence and presence of Fucaceae under an illumination of 240 Watt. 4 species of Fucaceae tested. Distance 100 cm.

	Variety *citrina*			Variety *olivacea*		
Group	1	2	3	1	2	3
No algae at inflow	108	2	2	48	1	0
	99	7	4	44	2	1
	77	1	6	23	1	0
	87	9	4	38	2	2
	85	2	0	9	0	0
Total number	456	21	16	162	6	3
No algae, total percentage	92.6	4.2	3.2	94.8	3.5	1.7
Fucus spiralis	58	6	15	11	2	2
	66	6	7	9	3	3
	71	2	8	14	0	2
	52	6	22	11	0	3
	55	4	20	12	0	3
Total number	302	24	72	57	5	13
Percentage	75.9	6.–	18.1	76.–	6.7	17.3
F. vesiculosus	77	13	39	34	7	19
	48	13	36	22	9	17
Total number	125	26	75	56	16	36
Percentage	55.3	11.5	33.2	53.3	12.1	33.3
Ascophyllum nodosum	61	4	21	4	3	3
	70	3	13	8	3	3
	60	10	17	10	2	1
	62	3	21	6	2	6
	61	7	20	6	1	5
Total number	314	27	92	34	11	18
Percentage	72.5	6.2	21.3	54.–	17.4	28.6
F. serratus	94	7	13	48	2	8
	66	7	13	9	2	5
	75	6	7	13	4	0
	73	4	12	12	1	4
	71	0	12	13	1	3
Total number	379	24	57	95	10	20
Percentage	82.4	5.2	12.4	76.–	8.–	16.–
Total all species	1120	101	296	242	42	87
Percentage	73.8	6.7	19.5	65.2	11.3	23.5

It follows from these data that:

1. All 4 species of Fucaceae clearly attract the snails from a distance of 100 cm. The percentage reaching the water inflow is 3 or less when no algae are there, on the average about 23 when algae are present. These figures are comparable with those obtained in VERWEY's experiments, in which it was found that 3.5 % of the snails reached the water inflow in the absence of Fucaceae, 22 % when they were there.
2. The percentage of snails reaching the algae from 100 cm distance differs for the various species of Fucaceae used. It is apparently greatest for *Fucus vesiculosus*, smallest for *Fucus serratus*, a point which will be considered in the next chapter.
3. There is probably no difference between the varieties *citrina* and *olivacea*, both reaching the algae in comparable numbers. This point is dealt with below.

2. SELECTION OF FUCACEAE FROM NEARBY

It was described in chapter II that snails were also given the choice between the 4 species of Fucaceae from nearby. The algae (see p. 375) were laid out in 4 portions in a circle, with the snails in its centre. The distance between the snails and the algae was about 15 cm. To keep both the algae and snails in good condition, water was kept slowly flowing over the bottom of the basin. Illumination was provided by a 60 Watt bulb. In all, 4 experiments were made, each experiment lasting 12 hours. After each experiment the circle of algae was turned 90°. The results are given in table IV.

TABLE IV

Movements of *Littorina obtusata* with 4 species of Fucaceae laid out in close proximity.

	Variety *citrina*						Variety *olivacea*					
Experiment	1	2	3	4	Total	%	1	2	3	4	Total	%
F. spiralis	31	7	1	32	71	29.1	6	2	0	4	12	29.3
F. vesiculosus	20	17	35	12	84	34.4	2	3	7	3	15	36.6
A. nodosum	3	26	5	5	39	16.–	1	4	2	0	7	17.1
F. serratus	5	18	12	15	50	20.5	0	2	2	3	7	17.1
Total number of snails	59	68	53	64	244	100.–	9	11	11	10	41	100.1

These results indicate that *Fucus vesiculosus* attracts more snails than the other species, *Ascophyllum nodosum* fewest. The outcome differs for the separate experiments, however, and it seems unlikely that the relative values for the different algal species would be the same if the number of experiments had been greater. The results for *olivacea*, moreover, are based on very small numbers of animals.

Further, the data do not indicate that the two varieties behave differently, they rather indicate that they behave in the same way. The results will be considered in more detail in the next chapter.

IV. CONCLUSIONS

I. ATTRACTION FROM A DISTANCE

The data obtained in the first series of experiments (attraction from some distance) suggest that *Littorina obtusata* is not very mobile in complete darkness and that it does not react much to Fucaceae in its neighbourhood when there is no light. Since the snail avoids strong light it is probable that it has a preference for light of intermediate strength.

If the quantity of light is sufficient all 4 species of Fucaceae attract the snail from a distance of 1 m. The attraction differs for the various species of algae and the results indicate that for both varieties of the snail the order of attraction by the algae is the same.

An overall χ^2-test was applied to the data, which to that end were arranged in a 2 × 8 table:

	L. citrina				*L. olivacea*				
	F. spir.	*F. vesic.*	*Ascophyll.*	*F. serr.*	*F. spir.*	*F. vesic.*	*Ascophyll.*	*F. serr.*	Total
On algae	72	75	92	57	13	36	18	20	383
Not on algae	326	151	341	403	62	72	45	105	1505
Total	398	226	433	460	75	108	63	125	1888

Calculation produced a $\chi^2 = 66.80$, which for 7 degrees of freedom means that it is highly unlikely that the results found could have been obtained if the different algae had exerted an equal attraction on the snails.

Thereupon, all combinations were compared separately in 2 × 2 tables by means of the Fisher-Yates test.

This is a parameter free significance test for binomial variates, which is, unlike the χ^2 test, valid for large as well as for small numbers. For small numbers this test has been tabulated by FINNEY (1948), whereas larger samples can be treated with the approximation given by FISCHER (1948, p. 96). The computation of one set is given by way of example.

L. citrina	On algae	Not on algae	Total
F. serratus	$a = 57$	$A - a = 403$	$A = 460$
F. spiralis	$b = 72$	$B - b = 326$	$B = 398$
	$a + b = 129$	$A + B - a - b = 729$	$A + B = 858$

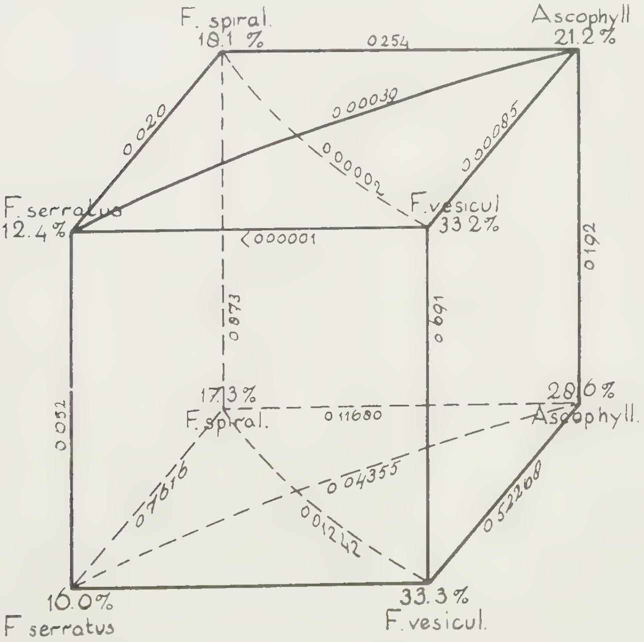
On the assumption of equal attraction by the two types of algae the expectation value of a is $\tilde{a}\ \frac{A \cdot (a+b)}{A+B} = \frac{460 \cdot 129}{858} = 69.161$

$$\sigma_a = \sqrt{\frac{A \cdot B \cdot (a + b) \cdot (A + B - a - b)}{(A+B)^2 \cdot A+B-1)}} = \sqrt{\frac{460 \cdot 398 \cdot 129 \cdot 729}{858^2 \cdot 857}} = 5.224$$

The deviation of a from its expectation value $= 69.161 - 57 = 12.161$, which amounts to 2.33 times its own standard deviation. According to the tabulation of the normal distribution this corresponds to a (bilateral) tail error value of $P = 0.020$, in others wordts to a significance level of 2 %.

The resulting levels of significance are represented in a pictorial form in figure 2. The data for variety *citrina* are given in the upper, those for *olivacea* in the lower half of the cube. Percentual frequencies of arrival of the snails on the various species of algae are given at the

VAR. CITRINA



VAR. OLIVACEA

Fig. 2. For explanation see text.

corners of the cube. Levels of significance between these latter figures are denoted along the connections: those in the horizontal planes refer to the difference in preference of one variety for different algae, those along the vertical edges to the differences in preference between the two varieties of the snail for a given algal species.

The differences in the horizontal planes are significant except those between *Fucus spiralis* and *Ascophyllum nodosum* in regard to variety *citrina*, between *F. spiralis* and *F. serratus*, between *F. vesiculosus* and *A. nodosum*, and between *F. spiralis* and *A. nodosum* in variety *olivacea*. The data for *citrina*, however, because of their greater numbers, can be considered more reliable than those for *olivacea*, and we may therefore conclude that both varieties of the snail are attracted by the four species of Fucaceae from a distance of 1 m in this order:

1. *Fucus vesiculosus*
2. *Ascophyllum nodosum*
3. *Fucus spiralis*
4. *Fucus serratus*

The data along the vertical edges do not indicate any significance and therefore indicate no difference in behaviour between the varieties[1].

It may be remembered that the experiments in the dark produced indications that *F. spiralis* caused a higher percentage of snails to move upstream than did *vesiculosus*, whereas the later experiments show that *F. vesiculosus* attracts a higher percentage than *F. spiralis* (33 against 18 %). The distances between the snails and the algae and the quantities of algae used in the two series of experiments were not the same, however, and it is not certain whether it is permissible to compare the figures for "upstream" in the earlier experiments with those found for "snails on algae" in the later ones. It is not impossible that in our experiments besides qualitative differences also quantitative differences in scent played a role and that with increasing distances maximum attraction shifted from one algal species to another, because the quantitative influence (strength of scent) interfered with the qualitative one (kind of scent). In view of the results obtained by others (BRAAMS and GEELEN, 1953; DAVENPORT, 1950- '53) one might be inclined to assume, however, that quality (specificity) of scent is most important.

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[1] It is worth pointing out expressly that it is remarkable in itself that the frequency of the reaction of an animal to the scent emitted by one of the species it feeds upon can be used to prove small differences in the quality of the scent. One would rather expect that the snails, when hungry, might react to a 100 % degree, when not hungry stay where they are, and that these differences would make it impossible to find averages for a certain food species. That this is not the case proves that a more or less constant percentage of the total is attracted by the scent characters. The same was found to be the case in nudibranch slugs feeding on sea anemones (BRAAMS and GEELEN, 1953).

2. ATTRACTION FROM NEARBY

It was stated in the foregoing chapter that the second series of experiments, in which the snails were given the choice between nearby algae, demonstrated that the snails were most attracted by *Fucus vesiculosus*, least by *Ascophyllum nodosum*. The results, however, varied a great deal in the different experiments (table IV). Moreover, the data for *olivacea* relate to too few animals. For this reason a restricted validity should be attributed to these results.

These data do not lend themselves to statistical treatment. The only test, which would meet the situation, would be the method of m-rankings (KENDALL, 1948, chapter 6, p. 80). In this test, however, the data only count for their rank, whereas numerical values do not enter into the computation. This is especially unfavourable in our case, since the numbers of snails in each experiment would not be accounted for. No adequate test is at present available. The experiment should be repeated so many times that the preference can be statistically ascertained.

It does attract attention, however, that there is an apparent disagreement between the results of the experiments of the first and the second series. In the second series (snails at a short distance from the algae) *Fucus spiralis* attracts a higher, *Ascophyllum nodosum* a lower percentage of snails than in the first series (snails at 1 m distance), as follows from table V.

TABLE V

Attraction at 1 m distance compared with choice from nearby (data from tabel III and IV).

Attraction from 1 m			Attraction from nearby (0.15 m)		
Algal species	*citrina*	*olivacea*	Algal species	*citrina*	*olivacea*
F. vesiculosus	33.2	34.6	*F. vesiculosus*	34.4	36.6
A. nodosum	21.2	28.6	*F. spiralis*	29.1	29.3
F. spiralis	18.2	17.3	*F. serratus*	20.5	17.1
F. serratus	12.4	16.–	*A. nodosum*	16.–	17.1

When the experiments were initiated it was believed that the question, whether the two varieties of *Littorina obtusata* would show different reactions to the scent of certain species of Fucaceae, could best be solved by using two different methods. Afterwards it was realized that the second method was probably inadequate, as taste qualities may have interfered with scent. The results of the two series of experiments can be brought into agreement if we assume that *Fucus spiralis* emits a scent which attracts a lower percentage of snails from 1 m distance than the scent emitted by *Ascophyllum nodosum*, but that *Fucus spiralis* is preferred as food because of its softness (or for another reason), whereas *Ascophyllum* is liked less by the snail on account of its hardness (or for some other reason). It seems natural that at some distance the snail is led by scent, whereas at close quarters scent and taste (structure of the algae included) may both play a role. This would mean that the results of the two series of experiments are not directly comparable. BARKMAN came to the conclusion that taste does not play a role, but this seems improbable.

In connection with the difference in preference shown by the snails for algae at some distance and nearby algae, the results of an experiment by BARKMAN will be reproduced here. It has been stated above that the second method (algae in a circle, with the snails in the centre) was copied from BARKMAN. He made only one such an experiment, but since he used 125 *citrina* and 100 *olivacea* its outcome must have had some significance.

TABLE VI

Selection of algae at close quarters. Data from our table IV, compared with those of BARKMAN's table XXIX.

	VAN DONGEN, table IV		BARKMAN, table XXIX	
	citrina	*olivacea*	*citrina*	*olivacea*
F. spiralis	29.1	29.3	21.6	25.8
F. vesiculosus	34.4	36.6	7.2	9.3
A. nodosum	16.–	17.1	25.6	25.8
F. serratus	20.5	17.1	45.6	39.2

It follows from this table that, whereas in my experiment most of the snails were found on *Fucus vesiculosus*, and *Fucus spiralis* took the second place, in BARKMAN's experiment *F. serratus* attracted by far the greatest number of snails, both varieties behaving similarly in this respect. In none of my 4 experiments did *F. serratus* attain the maximum number. Though I cannot give an explanation of this incongruity I am inclined to assume that the duration of the experiment may have had something to do with it, BARKMAN recorded the performance of his animals after 48 hours (two days), I myself after 12 hours. For two reasons the animals may gradually shift from one algal species to another:

1. Because they may gradually reach the alga liked best; Verwey got the impression that the snails, when fed both *serratus* and *vesiculosus*, were most of the time more numerous on *serratus*, presumably because the latter might be liked because of its softness.
2. Because they might disappear from a certain species when the latter is no longer fresh.

It might thus be a matter of time whether we find most snails on *serratus* or another species and what order of frequency we find. The above data do not suffice, however, to go further into the matter.

Barkman also made observations on the preference of the snails for the different species of Fucaceae under conditions different from those described above (Barkman, 1955, p. 38–41, tables xxv–xxvii). He used snails collected on different species of Fucaceae and noted their distribution over a number of algae after 3½–7 days. His data are summarized in table vii.

TABLE VII

Selection of algae at close quarters. Data from Barkman's tables xxv–xxvii.

	Variety *citrina*				Variety *olivacea*			
	collected on				collected on			
—	*F. vesiculosus*		*F. serratus*		*F. vesicolosus*		*Ascoph. nodosum*	
	number	%	number	%	number	%	number	%
F. spiralis	69	30.4	55	23.3	94	32.–	88	27.6
F. vesiculosus	46	20.3	68	28.8	39	13.3	97	30.4
Ascoph. nod.	42	18.5	32	13.6	93	31.6	64	20.1
F. serratus	70	30.8	81	34.3	68	23.1	70	21.9
Total	227	100.–	236	100.–	294	100.–	319	100.–

The results were difficult to account for, and Barkman, who considered them of doubtful value, tried to make a number of corrections. The chief point, however, is that these results show little agreement with the data found by Barkman and myself, given in table vi. There may be several reasons for this discrepancy, but Barkman's conclusions contain a supposition that may be of interest in this connection. He found that it looks as if snails of the variety *olivacea*, when collected on *F. vesiculosus*, appear to have a dislike for that species, and when collected on *A. nodosum*, might have a dislike for the latter. In other words, it seemed as if the animals like variation in their food. Though Barkman's results for variety *citrina* do not point in the same direction, a preference for variation in food might well play a secondary role.

It seems certain, however, in view of the experiments made by Barkman and myself, that the food preference of the snail does not agree with its attraction to the different algae by scent. Further, the facts do not indicate that there is a difference in either food or scent preference between the two varieties.

V. SUMMARY

Specimens of the snail *Littorina obtusata* are attracted by the scent of Fucaceae from a distance of 1 m. The attraction is strongest for *Fucus vesiculosus*, smallest for *Fucus serratus*. It is not certain that this difference is caused by the quality of the scent, but this appears probable. There is probably no different reaction to scent in the two varieties of the snail: *citrina* and *olivacea*.

Attraction caused by Fucaceae at a short distance apparently differs from that at 1 m. It is probable that at a distance of 1 m the snail is led by scent, whereas at close quarters scent and taste may both play a role; taste (structure of algae included) may lead to a preference different from that produced by scent.

The observations indicate that the snails are more active in light than in darkness.

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THE FUNCTIONAL MORPHOLOGY OF THE HEAD OF THE COMMON VIPER

Vipera berus (L.)

by

P. DULLEMEIJER

(*Zoological Laboratory, Leiden*)

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I. INTRODUCTION

The conception whereby the skull is considered as built of several functional components forming a totality, in which the components have a restricted individuality (Van der Klaauw, 1945, 1950), raises a number of problems and difficulties.

The first difficulty exists in the use of the concept: restricted individuality. If the components are fully incorporated in the wholeness of the organism and the distinction of the functional components occurs arbitrarily, then the presence of any individuality is questionable. If, however, in the case of a less complete incorporation, the functional components have their own individuality—in restricted form—, then the problem arises how far the restriction of this individuality may reach and what would be the relation of the component to the whole.

The second difficulty lies in the determination and distinction of the functional components. With the term functional component is meant a morphological structure of elements which has a certain function. Generally such a component shall not be restricted to the skeletal parts of the head, but shall embrace the weak parts too. The elements constituting the skull cannot be distinguished as functional components because these elements are mostly parts of them. The consequence is that the components influencing the skull do not all lie within the skull, but are partly situated outside and around it.

Connected with the problem of the distinction of the functional components is the question at which level these components can be distinguished or, in other words, at which level the morphological elements may be considered functional components.

Dependent on the level of distinction the following terms can be used. The term functional components is reserved for a general terminology. Thus functional components can be distinguished on different levels. The term apparatus will be used for the greater functional components, whereas the term constructions is utilized for parts in an apparatus.

Since it is possible to distinguish the functional components on these different levels, the problem arises whether parts of components, *in casu* constructions or parts of constructions, or entire apparatus must be integrated with others to a wholeness. It seems indeed valuable to do it on every level. So it may occur that only the skeletal elements in a construction can be integrated to a whole. The way in which the integration and correlation occurs is, however, quite different on different levels, so that a special research must be made concerning this problem. On the other hand, in principle the situation may occur that the elements of different constructions are very loosely correlated, but in the meantime highly dependent on the functional components, which are strongly correlated. Nevertheless, the integration of components on a lower level is in many cases problematic. Therefore it is much more reasonable to consider the entire head and the division of it into functional components than a part which can only be distinguished in the morphological property of its elements, *e.g.* the skeletal elements. The shape of the components can be understood now from rules existing between form and function. The term "rules" indicates the always, or frequently simultaneous occurrence of a certain form with a certain function. The attempt to discover these rules needs two different methods.

In the first of these, a comparative method, the functional components of the different species are compared. The result is a general rule which can be given in a correlation formula, *e.g.* aponeurotic attachment occurs on cristae, big animals have a relatively small brain.

The drawbacks of this method are: the difficult determination of the comparable functional components, the difficult division of comparable elements within these components, which occurs arbitrarily and the difficult determination of the influence of the surrounding elements. Concerning the last mentioned drawback it may be expected that functional components in different species will be surrounded by elements which differ in shape. These differently shaped elements shall have generally also different influences on the functional components. In other words, functional components in a different position in relation to their surrounding elements shall be influenced differently.

In the second, non-comparative method[1], the relation of the functional components to their function and the dependence of this relation on the surrounding elements, or in other words, on the available space for the component, is studied in one specimen (in fact many specimens of one species or a smaller taxon will be used). The shape and the structure of a component are considered a necessary deduction in constructive sense from some biological functions. In other words: the component is considered a realization of the function.

The necessity exists in the form of a correlation formula. This necessity possesses in many cases a certain degree of liberty. In those cases other factors than the realization of the function must be taken into account. In practice it is difficult or impossible to know the main function or the functions from which must be started. Therefore the reversed way is followed. The shape and structure is studied and the analysis leads to the functions, which are realized. This practical method must be followed by the theoretical deductive method to make the structure understandable.

The drawbacks of this method are the possibility of a high degree of liberty and the lack of knowledge of the function and of the correlation between form and function.

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[1] The fact that results of other fields of research are used, which are discovered by comparison, does not depreciate essentially this method.

Both methods complement each other, for on one hand the mutual influence of the functional components must be known in the comparative method, and on the other hand the correlation between form and function can be found by comparison.

In this study on the head of the viper the second method will be followed and complemented as far as possible by the first, mainly on the basis of a restricted knowledge of the structure of *Crotalus* and *Lachesis*.

The aim of this research is to understand the architecture of the entire head. The term architecture includes then the relation between the functional components in their spatial situation, whereas these functional components are considered as realizations of the functions.

In practice the description and the discussion of the form and the function must be given apart. As a matter of fact there follows from this an imperfection in the synthetical consideration due to the impossibility to consider form and function simultaneously in the description as well as in the discussion.

It must be remarked that the true comparative functional anatomy falls outside the field of this discussion. A true comparative functional anatomy is an anatomy based on the function-form relation in which the comparison is made between the architectonic patterns.

The common viper, *Vipera berus* (L.), has proved to be a good subject for this study, because of its extreme manner of food-intake and because of the fact that almost every part of the head may be adapted to this way of food-intake. Moreover, a number of movements of the bony parts are visible through the skin and can be analysed by measurements on moving-pictures.

II. MATERIAL

The material was obtained by the friendly help of Dr. H. Volsoe of the University of Copenhague, who sent a collection of heads of Danish vipers to Professor C. J. van der Klaauw. The heads were preserved partly in alcohol, partly in Bouin's fixative.

Dr. L. D. Brongersma of the Rijksmuseum van Natuurlijke Historie at Leiden was so kind as to place five living animals at my disposal. The specimens were caught in the province of Drente. Four of them died after a short time, one was examined when still fresh. One animal could be observed many times in the food-intake activities. Another living animal could be studied by the kind introduction of Dr. E. F. Jacobi, director, and the help of Mr. B. Bollee, attendant in the Zoological Garden Natura Artis Magistra in Amsterdam.

The material, preserved in alcohol 70%, was laid in water for some days before macroscopic dissecting. The macroscopic anatomy was traced out under a stereo-microscope, magnification 16 ×.

Two heads were cut in microscopical slides with the kind help of Dr. W. Vervoort of the Zoological Laboratory at Leiden. One head was preserved in alcohol, the other one in Bouin's fixative. Decalcification took place in 6% HNO_3. The sections were stained by haematoxylin-eosin. For the determination of the flexion resistance the transverse sections were drawn by means of a Zeiss-Winkel drawing prism on thick paper.

The determination of the flexion resistance occurred by partition of the drawing of a transverse section into small rectangles, of which the moment of resistance had been calculated to an axis through the centre of gravity and thereafter summarized for the entire surface of the transverse section. After that the moment of resistance could be compared with the flexion moment, at least, if the muscles attached to the bone work entirely. The centre of gravity for each transverse section was determined by free hanging on a needle along a vertical line of the transverse sections, imitated of thick paper.

For the application of mechanics were followed the principles pointed out by KLOPPER (1943, 1946) in his textbook on applied mechanics. The English terminology for mechanical phenomenons was borrowed from MURRAY (1936).

To get a good idea of the movements during the food-intake, two films were made of it by the "Universitaire Film" at Utrecht under the direction of MR. W. VAROSSIEAU. One of the films was made in infra-red light, because the viper did not strike the prey in fierce light. The swallowing of the kill was filmed in visible light. From the film-pictures a diagrammatical reconstruction could be made of the movements as well as of the direction and the velocity. Besides, the act could be reproduced many times if an observation had to be made during the morphological investigations. The poisoning act was filmed with slow-motion pictures (64 pictures/sec.). The attack, however, lasts about 1/30–1/40 sec., so that a rather indistinct picture arose.

The drawings showing the places of attachment of the muscles are made in the same way as those in numerous publications from the Zoological Laboratory in Leiden which appeared in the Proceedings of the Koninklijke Nederlandse Akademie van Wetenschappen. Joined places of attachment are separated by a line of crosslets. The places of attachment of the ligaments are indicated by a serrated line.

III. DESCRIPTION

Many authors have described the elements constituting the head of snakes. Some descriptions are also devoted to the common viper. So we may refer for a general description of the skeleton of snakes to VERSLUYS (1936), the muscular system to HAAS (1930) and LUBOSCH (1938), the glands to PHISALIX (1922) and FAHRENHOLZ (1937), the eye to FRANZ (1934) and the nose and surrounding parts to BROMAN (1918) and MATTHES (1934), *etc.* Nevertheless a detailed description of many parts is lacking, because these authors were interested in other problems. Therefore, after a general description a more detailed one will follow of the parts that are of importance for our problems.

A. THE SKULL (figs 1–11)

In the skull of the viper the main part is occupied by the cerebral skull. The ethmoidal region (fig. 4) joins it rostrally, the orbital one rostro-laterally. Ventral to the ethmoidal region and the cerebral skull the jaws are movably connected. Between the lower jaws are found the glottis and the tongue-bone.

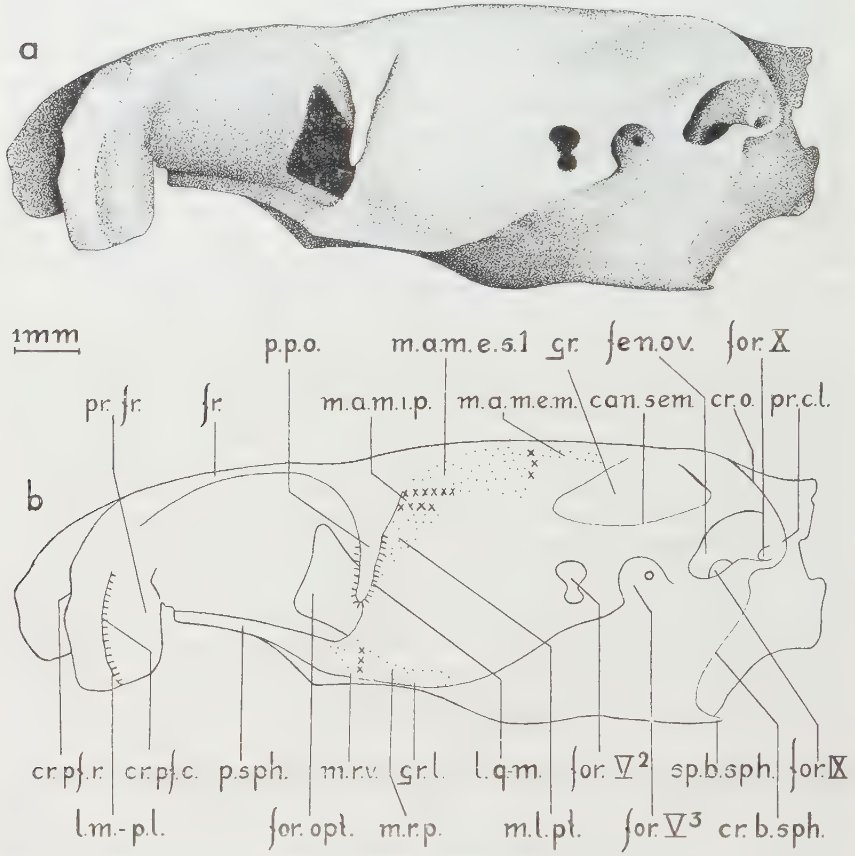


Fig. 1. Lateral view of the cerebral skull from left. a, drawn from nature; b, diagram. *can.sem.*, canalis semicircularis; *cr.b.sph.*, crista on the basisphenoid; *cr.o.*, crista occipitalis; *cr.pf.c.*, caudal crista on the praefrontale; *cr.pf.r.*, rostral crista on the praefrontale; *fen.ov.*, fenestra ovalis; *for.opt.*, foramen opticum; *for.V*^{2}, foramen nervi trigemini, ramus maxillaris; *for.V*^{3}, foramen nervi trigemini, ramus mandibularis; *for.IX*, foramen nervi glossopharyngei; *for.X*, foramen nervi vagi; *fr.*, frontale; *gr.*, groove between the canales semicirculares; *gr.l.*, lateral groove on the cerebral skull; *l.m.-p.l.*, ligamentum maxillo-praefrontale laterale; *l.q.-m.*, ligamentum quadrato-maxillare; *m.a.m.e.m.*, musculus adductor mandibulae externus medialis; *m.a.m.e.s.1*, musculus adductor mandibulae externus superficialis 1; *m.a.m.i.p.*, musculus adductor mandibulae internus pseudotemporalis; *m.l.pt.*, musculus levator pterygoidei; *m.r.p.*, musculus retractor palatini; *m.r.v.*, musculus retractor vomeris; *p.p.o.*, processus postorbitalis; *p.sph.*, parasphenoid; *pr.c.l.*, processus caudo-lateralis; *pr.fr.*, praefrontale; *sp.b.sph.*, spina on the basisphenoid.

The cerebral skull, including the otical region, is an almost cylindric bone, diminishing in breadth rostralwards between the orbitae and caudalwards to the foramen magnum.

The roof is flat (fig. 1). The caudo-lateral and caudal parts of the roof lie at a more ventral level (fig. 3). The surfaces of both parts have a triangular shape. The sides of the triangle of the caudo-lateral part are formed by the bony walls of the canales semicirculares *(can. sem.)*, leaving a shallow groove *(gr.)* between each other. The lateral side, formed by the lateral semicircular canal, runs in a straight rostro-caudal direction. The other sides are directed from latero-rostral to medio-caudal and from medio-rostral to latero-caudal.

The tops of the triangles of left and right do not meet each other in the dorsal median.

The caudal sides of the just mentioned left and right triangles form the rostral side of a caudal triangular part. The third side of this caudal triangular part is formed by the caudal border of the cerebral skull, *i.e.* the dorsal edge of the foramen magnum. This caudal triangular part lies on a more ventral level than the first.

Rostrally the left and right sides of the cerebral skull are concave where they coincide with the orbital wall. Caudal to the orbita the side is spherical. Caudally this spherical part is neighboured by the area in which lie the foramina nervi trigemini et facialis *(for.* V^2, V^3 and *VII)*. The caudal part of the lateral wall is formed by the canalis semicircularis lateralis. The wall between statical organ and brain will be described later on in the chapters devoted to those regions.

The bottom of the cerebral skull has an irregular outer surface (figs 1 and 2). The parasphenoid *(p. sph.)* lies as a flat rhomb-shaped bone, bordered by cristae *(cr.p.sph.)* caudo-medial to and between the orbitae. Caudal to this rhomb-shaped area the ventral surface of the cerebral skull is broadened and spherical. About 2 mm rostral to the foramen magnum the surface runs dorsalwards. The outer shape of the bottom of the cerebral skull is conical. At the most ventral place of the bottom lies a low transverse crista *(cr.b.sph.)*, ending paramedial in a paired spina *(sp.b.sph.)*, which is directed caudalwards.

The orbita is relatively large. The rostral and the dorso-medial wall are formed by the concave parts of the praefrontale *(pr.fr.)*, resp. the frontale *(fr.)*. Caudally the thin processus postorbitalis *(p.p.o.)* forms the border. The other sides are not covered by bones.

The capsula ethmoidalis of each side (fig. 4) consists of a hollow hemisphere, surrounded by thin bone or cartilaginous septa. The medial wall of both sides is formed by a thin septum, continuing in the triangular bony part of the roof. Rostrally the septum bears on both sides a transverse processus *(pr.tr.)*, forming the most rostral part of the ventral wall. The bony ventral wall consists furtheron only of the caudal part. It is a flat triangular plate *(tr.pl.)*, bending dorsalwards, thus form-

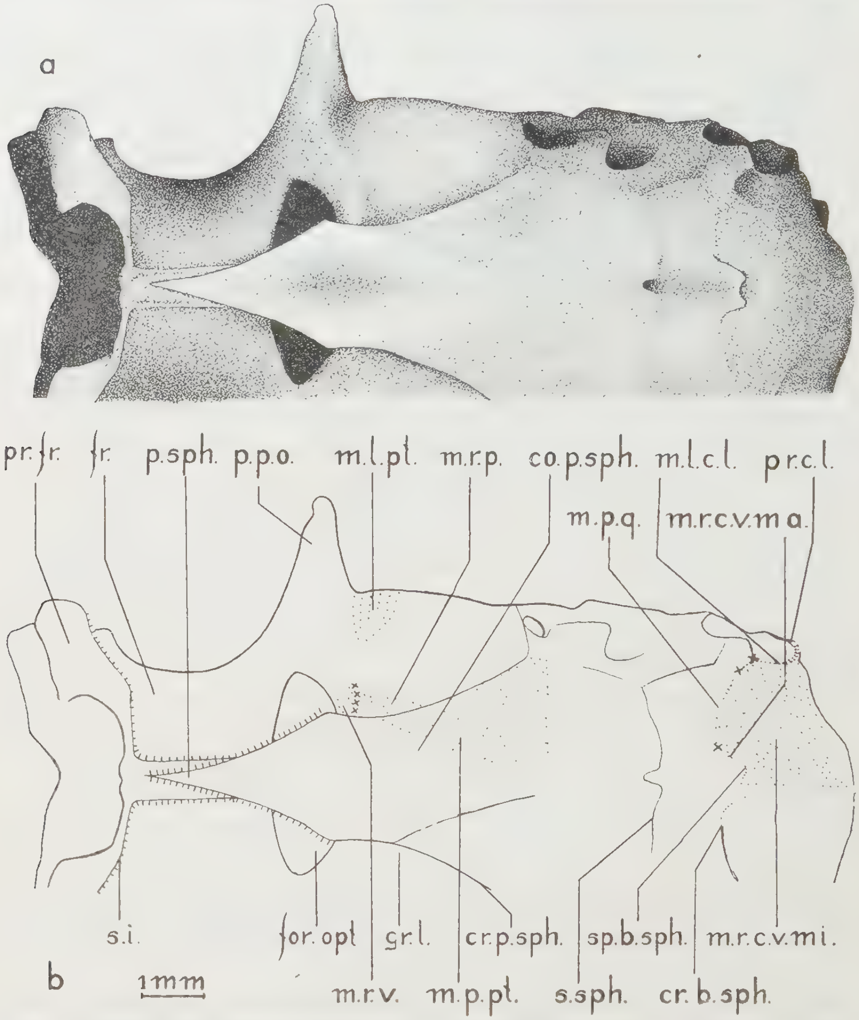


Fig. 2. Ventral view of the cerebral skull. a, drawn from nature; b, diagram. *co.p.sph.*, costa on the parasphenoid; *cr.b.sph.*, crista on the basisphenoid; *cr.p.sph.*, crista on the parasphenoid; *for.opt.*, foramen opticum; *fr.*, frontale; *gr.l.*, lateral groove on the cerebral skull; *m.l.c.l.*, musculus longissimus colli lateralis; *m.l.pt.*, musculus levator pterygoidei; *m.p.pt.*, musculus protractor pterygoidei; *m.p.q.*, musculus protractor quadrati; *m.r.c.v.ma.*, musculus rectus capitis ventralis major; *m.r.c.v.mi.*, musculus rectus capitis ventralis minor; *m.r.p.*, musculus retractor palatini; *m.r.v.*, musculus retractor vomeris; *p.p.o.*, processus postorbitalis; *p.sph.*, parasphenoid; *pr.c.l.*, processus caudo-lateralis; *pr.fr.*, praefrontale; *s.i.*, septum interorbitale; *s.sph.*, sutura between the sphenoids; *sp.b.sph.*, spina on the basisphenoid.

ing the caudal part of the lateral wall *(c.l.w.)* beside the praefrontale. The caudo-lateral wall is formed by the concave praefrontale. The other parts of the sides are membranous or cartilaginous.

The bony capsule of the organ of Jacobson joins the regio ethmoi-

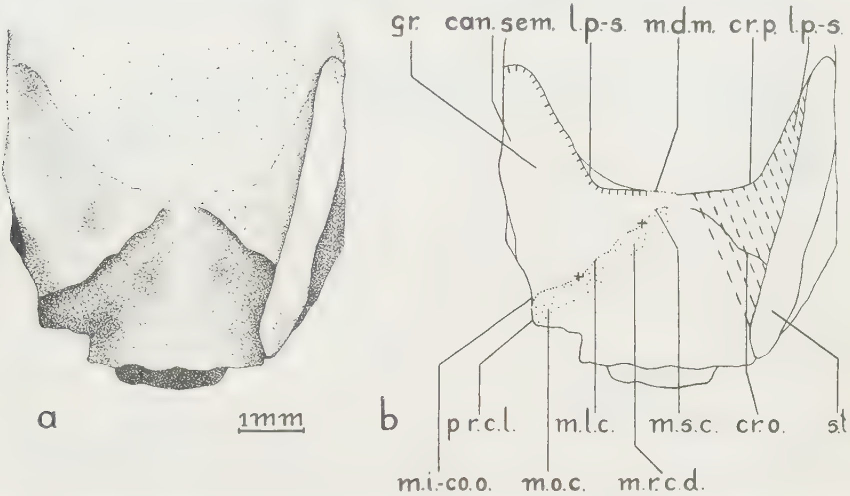


Fig. 3. Dorsal view of the caudal part of the cerebral skull. a, drawn from nature; b, diagram. *can.sem.*, canalis semicircularis; *cr.o.*, crista occipitalis; *cr.p.*, crista parietalis; *gr.*, groove between the canales semicirculares; *l.p.-s.*, ligamentum parieto-supratemporale; *m.d.m.*, musculus depressor mandibulae; *m.i.-co.o.*, musculus iliocostalis occipitalis; *m.l.c.*, musculus longissimus capitis; *m.o.c.*, musculus obliquus capitis; *m.r.c.d.*, musculus rectus capitis dorsalis; *m.s.c.*, musculus spinalis capitis; *pr.c.l.*, processus caudo-lateralis; *s.t.*, supratemporale.

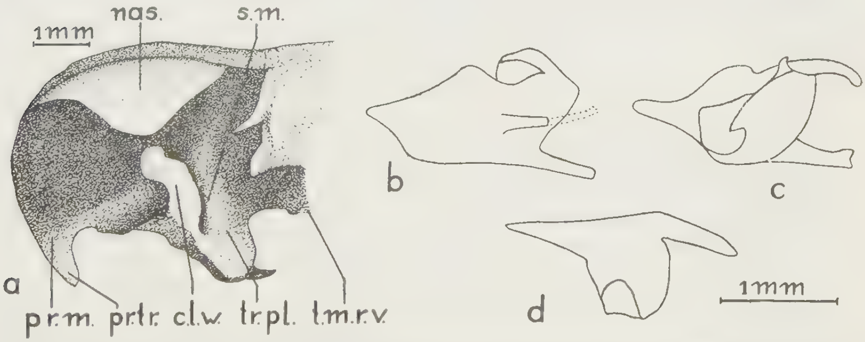


Fig. 4. a. Lateral view of the bony olfactorial capsule. b. Ventro-medial view of the left vomer. c. Dorso-lateral view of the right vomer. d. Dorsal view of the left septomaxillare. *c.l.w.*, caudal part of the lateral wall, formed by the dorsal directed wing of the septomaxillare; *nas.*, nasale; *pr.m.*, praemaxillare; *pr.tr.*, processus transversus rostralis of the praemaxillare; *s.m.*, septomaxillare; *t.m.r.v.*, tendon of the musculus retractor vomeris; *tr.pl.*, transverse plate of the septomaxillare.

dalis caudo-ventrally. A detailed description will be given later on.

The upper jaw (figs 5 and 6) consists of many parts, movably connected with each other and with the above described part of the skull. Ventro-lateral to the regio ethmoidalis and movably connected with the praefrontale lies the maxillare *(m.)*. The maxillare resembles a trun-

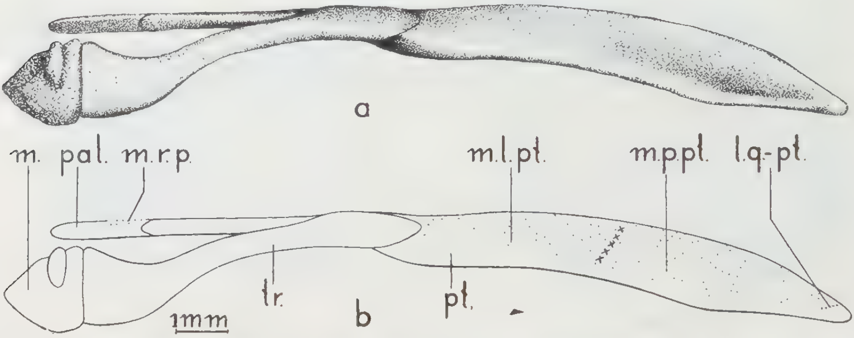


Fig. 5. Dorsal view of the left upper jaw. a, drawn from nature; b, diagram. *l.q.-pt.*, ligamentum quadrato-pterygoidale; *m.*, maxillare; *m.l.pt.*, musculus levator pterygoidei; *m.p.pt.*, musculus protractor pterygoidei; *m.r.p.*, musculus retractor palatini; *pal.*, palatinum; *pt.*, pterygoid; *tr.*, transversum.

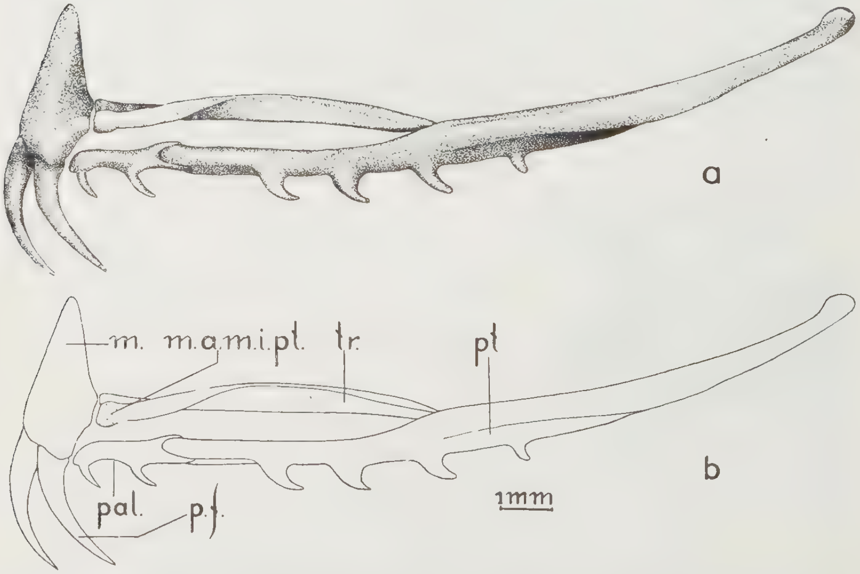


Fig. 6. Lateral view of the left upper jaw. a, drawn from nature; b, diagram. *m.*, maxillare; *m.a.m.i.pt.*, musculus adductor mandibulae internus pterygoideus; *p.f.*, poison-fang; *pal.*, palatinum; *pt.*, pterygoid; *tr.*, transversum.

cated prism, of which one face is directed rostro-laterally, the second face rostro-medially and the third caudally. The upper face is directed dorso-caudally and forms the articulation with the praefrontale. The lower face is directed ventro-caudally and bears the poison-fang (*p.f.*). A difference from the prismatic form is the fact that both the caudal edges curve a little inward and besides the other edges are not quite straight either.

The transversum *(tr.)* is movably connected with the maxillare, just below the place where the caudal edges of the maxillare curve inward. The transversum is a long flat bone, directed rostro-caudally and about 6 mm long. Rostrally it is about 2 mm broad, but halfway its length the breadth diminishes to about 1 mm. Caudally it lies upon the pterygoid *(pt.)*, with which it is slightly movably connected in a horizontal plane. The articular part of the transversum has the shape of a spatula.

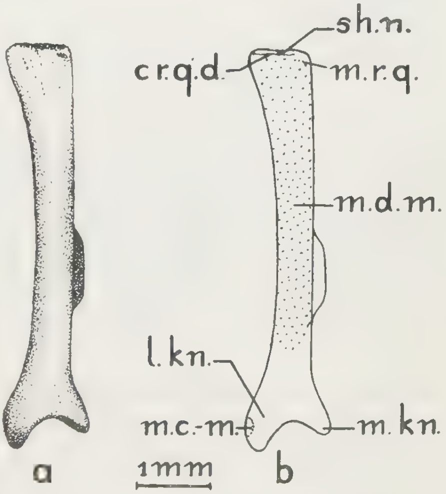


Fig. 7. Latero-caudal view of the left quadratum. a, drawn from nature; b, diagram. *cr.q.d.*, crista quadrati dorsalis; *l.kn.*, lateral knob of the joint; *m.c.-m.*, musculus cervico-mandibularis; *m.d.m.*, musculus depressor mandibulae; *m.kn.*, medial knob of the joint; *m.r.q.*, musculus retractor quadrati; *sh.n.*, shallow short nick.

The palatinum *(pal.)* is found medial to the maxillare. It is weakly attached to the maxillare by connective tissue and is only some mm long. It is a thin plate in the parasagittal plane and bears usually four teeth.

Behind the palatinum and tightly connected with it lies the pterygoid. The pterygoid is a long bone, reaching from a point under the orbita to a point latero-caudal to the foramen magnum, where it is connected with the quadratum.

The pterygoid can be divided into three parts:

The rostral part, as far as the place of connection with the transversum, has the same shape as the palatinum. The middle part is twice as broad as the rostral one and the caudal part is flat and broad in a latero-medial plane. This caudal part turns a little dorsalwards and does not bear teeth. In this part two grooves are formed. One groove, facing ventrally, lies medially; the other one, facing dorsally, lies laterally. Thus in a transverse section the pterygoid is wave-shaped. In the last caudal mm the bone narrows and forms a little knob for the articulation with the quadratum.

The quadratum *(q.)* is a long thin bone (figs 7 and 8), lying between the supratemporale and the lower jaw. It is a little flattened and in closed position of the mouth the lateral plane is facing latero-caudally and slightly dorsally. Dorsally it is somewhat broadened and flatter. The upper top is divided into two parts by a very short nick *(sh.n.)*. Ventrally it forms two knobs serving as an articulation with the lower jaw. Between these knobs lies a saddle-like basin. The lateral knob *(l.kn.)* is almost round. The medial knob *(m.kn.)* is smaller and flatter than the lateral one.

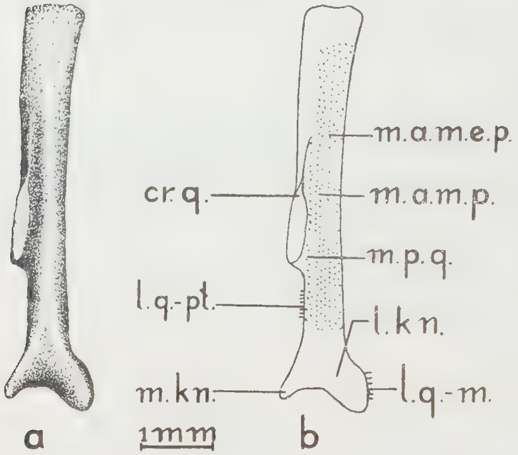


Fig. 8. Medio-rostral view of the left quadratum. a, drawn from nature; b, diagram. *cr.q.*, crista quadrati; *l.kn.*, lateral knob of the joint; *l.q.-m.*, ligamentum quadrato-maxillare; *l.q.-pt.*, ligamentum quadrato-pterygoidale; *m.a.m.e.p.*, musculus adductor mandibulae externus profundus; *m.a.m.p.*, musculus adductor mandibulae posterior; *m.kn.*, medial knob of the joint; *m.p.q.*, musculus protractor quadrati.

The supratemporale *(s.t.)* is an oblong flat bone (fig. 9). It is regular, only halfway the body it shows a point-shaped broadening, directed lateralwards.

The lower jaw *(l.j.)* can be divided into four regions (figs 10 and 11):

1. the in transverse section more or less round or ellipsoid rod forming the 'lower jaw itself'
2. the region which the teeth are placed in
3. a plate-shaped extension on the caudal part
4. the articulation with the quadratum.

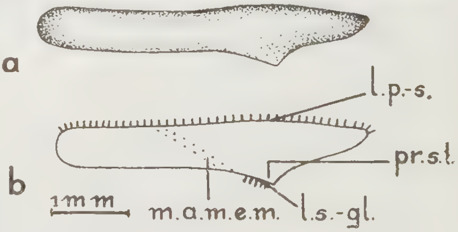


Fig. 9. Dorsal view of the left supratemporale. a, drawn from nature; b, diagram. *l.p.-s.*, ligamentum parieto-supratemporale; *l.s.-gl.*, ligamentum supratemporale-glandulare; *m.a.m.e.m.*, musculus adductor mandibulae externus medialis; *pr.s.t.*, processus supratemporalis.

The lower jaw is slightly curved. It is ring-shaped in a transverse section (fig. 44). The rostral part, bearing the teeth, is more or less flattened in a latero-medial direction and curves inward rostrally. Caudally this part consists of three irregularly shaped bony elements. The detailed description will be given later on.

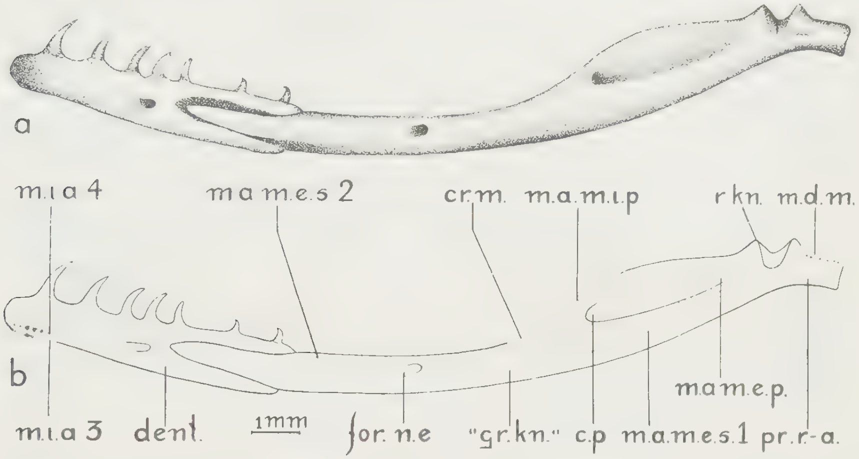


Fig. 10. Lateral view of the left lower jaw. a, drawn from nature; b, diagram. *c.p.*, canalis primordialis; *cr.m.*, crista mandibularis; *dent.*, dentale; *for.n.e.*, foramen nervi trigeminir,amus musculus externus; "*gr.kn.*", "Groszknochen"; *m.a.m.e.p.*, musculus adductor mandibulae externus profundus; *m.a.m.e.s.1*, musculus adductor mandibulae externus superficialis 1; *m.a.m.e.s.2*, musculus adductor mandibulae externus superficialis 2; *m.a.m.i.p.*, musculus adductor mandibulae internus pseudotemporalis; *m.d.m.*, musculus depressor mandibulae; *m.i.a.3*, musculus intermandibularis anterior 3; *m.i.a.4*, musculus intermandibularis anterior 4; *pr.r.-a.*, processus retro-articularis; *r.kn.*, rostral knob of the joint.

The articular surface with the quadratum is saddle-like. The knobs are placed before each other. Rostral to the articular surface is a flat extension placed on the jaw. Lateral to this extension lies the aperture of the canalis primordialis *(c.p.)*.

The part caudal to the articular surface is more or less quadrangular and a little curved inward (fig. 13).

The tongue-bone consists of two long thin rods, which are rostrally connected. The corpus hyale is triangular and bears a rostrally directed processus.

B. THE MUSCLES

Many authors have studied the muscles of snakes. Most descriptions are devoted to the muscles related with the venomous apparatus (Phisalix, 1922; Wolter, 1924; Radovanovic, 1928, 1935; Haas, 1930, a.o.), or to the intermandibular muscular system (Lubosch, 1933). There are no special detailed data on the muscular system in *Vipera berus*.

In this description the terminology of LAKJER (1926) has been followed.

1. *Musculus adductor mandibulae externus superficialis* (figs 1, 10, 11 and 14; *m.a.m.e.s. 1,2)*

This muscle is divided into two parts.

The first part runs as a flat bundle from the region behind the eye straight to the lower jaw (figs 1 and 10). It passes through the inner side of the curve of the second part.

The place of attachment in the region on the cerebral skull has a somewhat triangular shape. From the base of the processus postorbitalis *(p.p.o.)* runs a smoothly curving line into a caudo-medial direction. This line bends about 3 mm farther caudo-laterally and ends close to the rostral point of the supratemporale. It is a weak imprint and forms the border between an almost dorsally facing part of the cerebral skull without any muscle attachment, and a rounded part of the cerebral

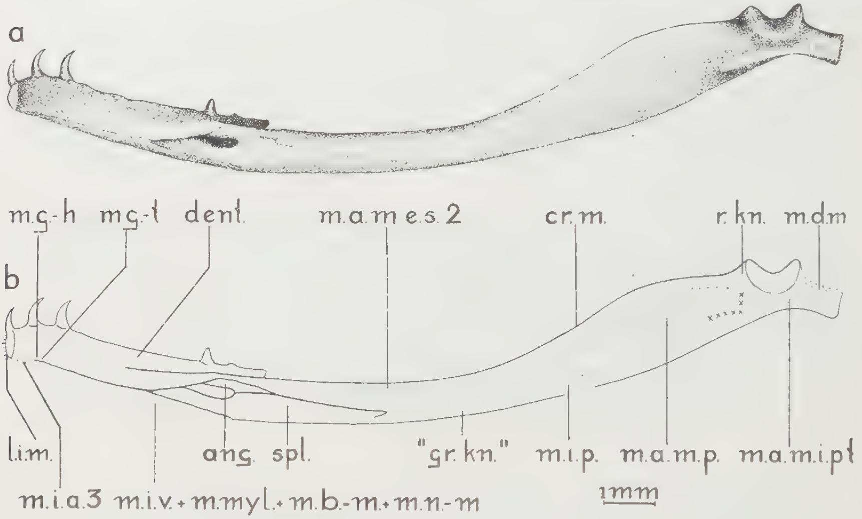


Fig. 11. Medial view of the right lower jaw. a, drawn from nature; b, diagram. *ang.*, angulare; *cr.m.*, crista mandibularis; *dent.*, dentale; "*gr.kn.*", "Groszknochen"; *l.i.m.*, ligamentum intermandibulare; *m.a.m.e.s.2*, musculus adductor mandibulae externus superficialis 2; *m.a.m.i.pt.*, musculus adductor mandibulae internus pterygoideus; *m.a.m.p.*, musculus adductor mandibulae posterior; *m.b.-m.*, musculus branchio-mandibularis; *m.d.m.*, musculus depressor mandibulae; *m.g.-h.*, musculus genio-hyoideus; *m.g.-t.*, musculus genio-trachealis; *m.i.a.3*, musculus intermandibularis anterior 3; *m.i.p.*, musculus intermandibularis posterior; *m.i.v.*, musculus intermandibularis ventralis; *m.myl.*, musculus mylohyoideus; *m.n.-m.*, musculus neuro-mandibularis; *r.kn.*, rostral knob of the joint; *spl.*, spleniale.

skull, facing laterally, to which many muscles are attached. The place of attachment of this first part of the musculus adductor mandibulae externus superficialis reaches to the turn in the border-line mentioned above.

The ventral border of the place of attachment is not quite clear. The attachment finishes here on a line connecting the base of the processus postorbitalis with the most rostral point of the supratemporale. The fibres of the muscle do not reach the supratemporale, but end at a ¼ of the distance from the supratemporale.

The caudal border, the third side of the triangle, is a straight line lying at ¼ of the distance between the processus postorbitalis and the supratemporale, measured from the supratemporale.

The attachment to the whole area is musculous. The attachment to the smoothly curving line forming the dorsal border is rather strong, ventrally it is weak. The fibres are attached with acute angles. Sometimes the attachment to the smooth line is aponeurotic.

The place of attachment to the lower jaw is not demarcated by visible structures of the bone. It occupies the ventral part of the lateral surface of the lower jaw and reaches from a point just rostral to the joint between quadratum and jaw, to a point lying about 2 mm rostral to the foramen of the canalis primordialis *(c.p.)*. The place of attachment is quite narrow. The attachment is aponeurotic. The aponeurosis is a continuation of the periost of the outer side of the jaw, and it is tangentially attached. The fibres of the bundle diverge a little dorsalwards. In a few cases some medial fibres are musculously attached.

The second part of the musculus adductor mandibulae externus superficialis runs from the connective tissue around the glandula venenata to the lower jaw (figs 10, 11 and 14). The glandula venenata *(gl.ven.)* is an oblong oval gland, covered by firm connective tissue.

The place of attachment lies on the dorsal, the lateral and the laterocaudal plane of the connective tissue around the gland. An attachment to the medial side (WOLTER, 1924) does not occur in my material. It reaches rostralwards to about halfway the length of the gland; the position of the border-line *(bl.mf.)* is quite variable. Ventralwards the place of attachment extends as far as ¾ of the height of the gland.

The attachment is musculous.

The place of attachment to the lower jaw is not clearly determined. It is a line starting close and rostral to the dorsal extension of the lower jaw. Rostrally the line reaches the caudal tooth laterally, but it never crosses the border-line between the "Groszknochen" *("gr.kn.")* and the dentale *(dent.)*.

The attachment to this line is aponeurotic. The aponeurosis is formed by a continuation of the periost around the lower jaw. The fibres of the periost diverge a little and form a V-shaped gutter, which causes a lateral and a medial surface aponeurosis. This situation makes it understandable that WOLTER (1924) found a lateral place of attachment and HAGER (1906) a medial one.

The muscle fibres, when starting from the glandula venenata, run parallel to each other into a caudal direction. They turn caudally around the gland and are further on directed rostro-ventrally. In closed position of the jaw the fibres run almost parallel to the jaw. The fibres, which converge a little near the jaw, are attached to the aponeurosis.

In some cases the way of attachment differs from the described situation (figs 10 and 11). The fibres run on up to the lower jaw between both surface aponeuroses. The place of attachment consists in this case of a narrow area, bordered by a medial and a lateral tangential aponeurotic attachment. Between the aponeuroses the attachment is musculous.

2. *Musculus adductor mandibulae externus medialis* (figs 1 and 9; *m.a.m.e.m.*)

This muscle runs from the cerebral skull and the supratemporale to the lower jaw and the corner of the mouth.

The place of attachment on the cerebral skull and the supratemporale is all but restricted to that part of the weak imprint, caudal to the curve described at the above mentioned muscle. This imprint continues on the supratemporale as far as the joint with the quadratum. The place of attachment is very narrow and the attachment is musculous.

On the lower jaw the muscle is aponeurotically attached to the medial plane of the aponeurosis of the second part of the musculus adductor mandibulae externus superficialis. In the case of a musculous attachment of the forementioned muscle, the aponeurosis of the musculus medialis runs on to the lower jaw. Before reaching the aponeurosis of the musculus superficialis the aponeurosis of the musculus adductor mandibulae externus medialis branches off a small part to the corner of the mouth.

The muscle is broad and flat. The fibres run ventrally and somewhat rostrally. Ventralwards the muscle becomes cylindric. Close behind the corner of the mouth it curves rostrally.

3. *Musculus adductor mandibulae externus profundus* (figs 8, 10 and 14; *m.a.m.e.p.*)

This muscle runs from the quadratum to the caudal part of the lower jaw before the articulation and to the glandula venenata.

The border of the area of attachment of the musculus adductor mandibulae externus profundus lies lateral to a crista *(cr.q.)*, at a short distance, and medial to the most lateral line of the quadratum when the mouth is closed. This crista (*cr.q.*) lies halfway the length of the body of the quadratum. It stands on the plane facing rostrally and is directed medio-rostrally. It runs parallel to the longitudinal axis of the quadratum. A sharp demarcation between the place of attachment of the musculus adductor mandibulae externus profundus and that of the musculus adductor mandibulae posterior, which lies between the crista *(cr.q.)* and this muscle, does not exist. The dorsal and ventral borders of the place of attachment are rather variable. They are formed by the cartilage surrounding the ventral and dorsal parts of the quadratum. It must be mentioned here that there is no attachment to the cartilage itself. The muscle fibres are attached to this area with almost right angles.

The lower jaw shows at its caudal part a plate-shaped extension, directed dorsalwards and a little medially. This extension stands on the medio-dorsal side of the lower jaw, which is in transverse section almost circular or ellipsoid. In the groove between the plate-shaped extension and the lower jaw itself opens the canalis primordialis *(c.p.)*. The extension begins at 2 3 of the length of the lower jaw measured from rostrally and it ends in the rostral articular knob *(r.kn.)* on the lower jaw. The upper limit of the extension runs at first almost strictly dorsally, then turns after some mm caudalwards. A bending of the lower jaw, just below the rostral end of the extension, gives this extension a triangular or segmental form.

The area of attachment is bounded ventro-laterally by the attachment of the musculus adductor mandibulae externus superficialis part 1 and dorso-medially by the upper ridge of the extension mentioned above. Caudally the border is formed by the cartilage of the articulation and rostrally it reaches to the place of attachment of the second part of the musculus adductor mandibulae externus superficialis, *in casu* to the most rostral point of the extension.

The attachment to the lower jaw is musculous. The fibres are attached to the whole area of the described part of the lower jaw, the groove, a little to the extension and to the dorsal ridge of the extension.

The place of attachment on the glandula venenata is a small area situated ventro-caudally on the connective tissue covering the gland. Rostrally the muscle is divided by the ramus mandibularis nervi V into a lateral and a medial part. Caudally the muscle is undivided.

About half the fibres of the latero-rostral part that arise from the dorsal part of the quadratum do not reach the lower jaw. These fibres are attached to the glandula venenata and form a firm connection with it.

4. *Musculus adductor mandibulae posterior* (figs 8, 11 and 15; *m.a.m.p.*)

This muscle runs from the quadratum to the lower jaw.

The area of attachment on the quadratum cannot be separated from the area of attachment of the musculus adductor mandibulae externus profundus. It reaches from close and lateral to the crista *(cr.q.)* on the quadratum to the attachment of the musculous adductor mandibulae externus profundus. The area is very narrow and ends ventrally near the joint with the lower jaw. The attachment to the whole area is musculous.

The area of attachment on the lower jaw occupies almost the whole medial plane of the plate-shaped extension of the lower jaw. There is no attachment to the lower jaw itself. Dorsally the area of attachment ends at about 1 mm distance from the upper ridge of the extension. Rostrally the area begins some mm caudal to the most rostral point of the extension, where this extension turns a little laterally. The caudal limit is determined by the cartilage of the joint.

The attachment to the whole area is musculous and occurs for the majority of the fibres on the most ventral part. Dorsally the fibres reach the lower jaw with a sharp angle, so that the fibres are attached to the bone at relatively great distances from each other.

5. *Musculus adductor mandibulae internus pseudotemporalis* (figs 1, 10 and 15; *m.a.m.i.p.*)

This muscle runs from the cerebral skull to the lower jaw.

The area of attachment on the cerebral skull is very small, 0.5 × 0.1 mm, and lies ventral to the area of attachment of the first part of the musculus adductor mandibulae externus superficialis. This area is not clearly outlined. The fibres are musculously attached.

They run as a small bundle straight in a ventral, slightly caudal direction to the lower jaw.

The extension of the lower jaw shows at its rostral dorsal part a crista *(cr.m.)*, 4 mm long, which continues some mm rostralwards on the lower jaw. To this crista the muscle is aponeurotically attached.

The fibres of the aponeurosis diverge distinctly to this extension (fig. 15). The aponeurosis cannot be separated from the connective tissue of the corner of the mouth, with which the musculus pseudotemporalis and the musculus medialis are both connected.

Between the dorsal part of the musculus pseudotemporalis and the musculus externus run some branches of the nervus trigeminus.

6. *Musculus adductor mandibulae internus pterygoideus* (figs 6, 11, 12 and 16; *m.a.m.i.pt.* and *m.pt.acc.*)

This muscle runs from the transversum *(tr.)* and the pterygoid (*pt.*) to the lower jaw *(l.j.)*. Besides, a little bundle of fibres is attached to the connective tissue of the corner of the mouth, and to the connective tissue around the poison-fang.

The most rostro-lateral point of the transversum is slightly curved ventralwards and projects a little laterally. To this point is attached a tendon *(t.tr.)*, to which two strong bundles of the muscle are attached, a medial *(p.2)* and a lateral one *(p.1)*.

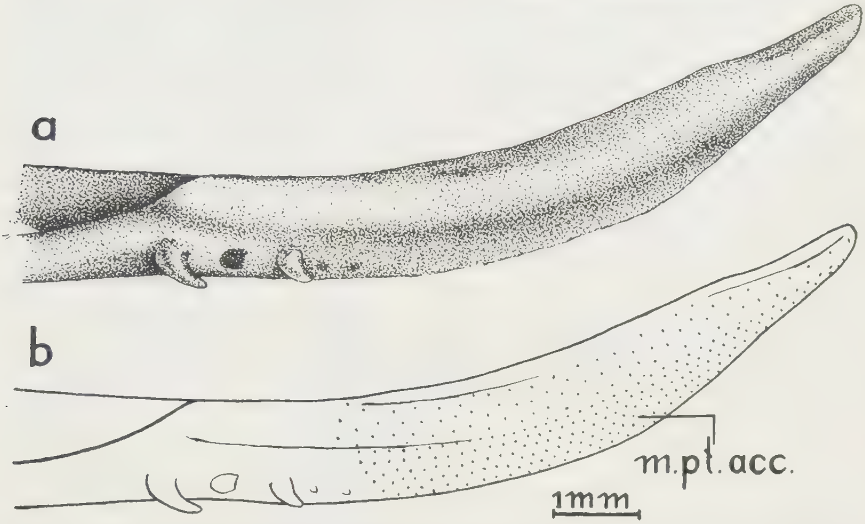


Fig. 12. Latero-ventral view of the caudal part of the left pterygoid. a, drawn from nature; b, diagram. *m.pt.acc.*, musculus adductor mandibulae internus pterygoideus accessorius.

The place of attachment on the pterygoid lies caudal to the teeth and along the whole breadth of the pterygoid on the ventral plane, mainly concentrated in the ventral groove (fig. 12). A short, big bundle is musculously attached to the whole plane.

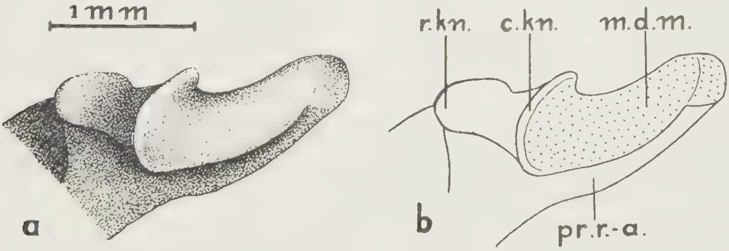


Fig. 13. Latero-dorsal view of the caudal part of the left lower jaw. a, drawn from nature; b, diagram. *c.kn.*, caudal knob of the joint; *m.d.m.*, musculus depressor mandibulae; *p.r.-a.*, processus retro-articularis; *r.kn.*, rostral knob of the joint.

Caudal to the teeth the pterygoid is wave-shaped in transverse section. It shows a medial groove, facing dorsally and a lateral one, facing ventrally.

The bundles, which can clearly be distinguished in the rostral attachment of the muscle, are caudally not or hardly to be separated.

The area of attachment on the lower jaw lies on the medial plane ventral to the joint. Close to the joint and ventral to it lies a groove, which has about the same length as the articular surface and is a little curved. Ventrally this groove is bordered by the round edge of the rod of the lower jaw itself. The ventral side of this edge is flat and is part of the area of attachment. Caudally the groove diminishes in depth and becomes a flat plane. Rostrally a separate place of attachment can be distinguished. It lies close and ventral to the most caudal place of attachment of the musculus adductor mandibulae posterior. It is a very small, almost pointed rough place.

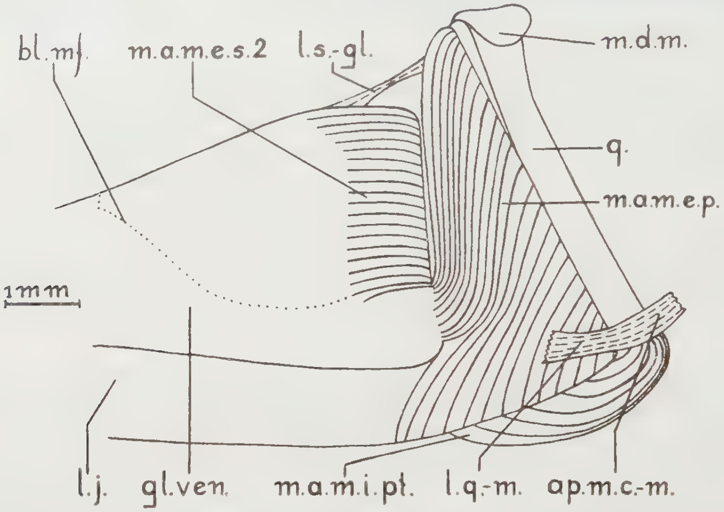


Fig. 14. Dorso-lateral view of the muscles, attached to the glandula venenata. *ap.m.c.-m.*, aponeurosis of the musculus cervico-mandibularis; *bl.mf.*, most rostral borderline of the muscle fibres; *gl.ven.*, glandula venenata; *l.j.*, lower jaw; *l.s.-gl.*, ligamentum supratemporale-glandulare; *l.q.-m.*, ligamentum quadrato-maxillare; *m.a.m.e.p.*, musculus adductor mandibulae externus profundus; *m.a.m.e.s.2*, musculus adductor mandibulae externus superficialis 2; *m.a.m.i.pt.*, musculus adductor mandibulae internus pterygoideus; *m.d.m.*, musculus depressor mandibulae; *q.*, quadratum.

The attachment to the whole area is musculous. Three all but inseparable parts can be distinguished: the first part is attached in the groove, and is caudally connected with the second one. This second part is attached to the ventral plane of the lower jaw. The third part is a small bundle and is attached to the small rough place, mentioned above.

A small aponeurosis *(ap.c.m.)* inserts rostrally in the connective tissue of the corner of the mouth. The fibres of this aponeurosis diverge rostralwards into the connective tissue.

The tendon running to the transversum branches off a small one to the connective tissue around the poison-fang.

Rostrally the muscle can be divided into four parts:

The first part *(p.1)* is attached to the transversum with a tendon *(t.tr.)*, and the fibres are running to the most rostral part of the place of attachment on the lower jaw. On a short distance from the lower jaw this part is a little narrowed and has formed an aponeurotic tissue on its surface.

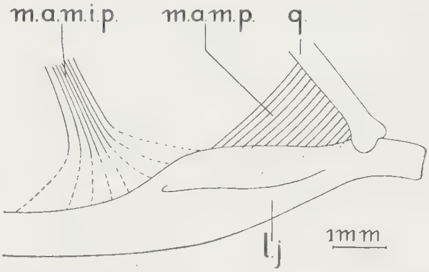


Fig. 15. Lateral view of the musculus adductor mandibulae posterior. *l.j.*, lower jaw; *m.a.m.i.p.*, musculus adductor mandibulae internus pseudotemporalis; *m.a.m.p.*, musculus adductor mandibulae posterior; *q.*, quadratum.

The tendon of the first part has a caudal continuation, to which the second part *(p. 2)* is attached. Close to the place of attachment on the lower jaw is this part not to be distinguished from the first part.

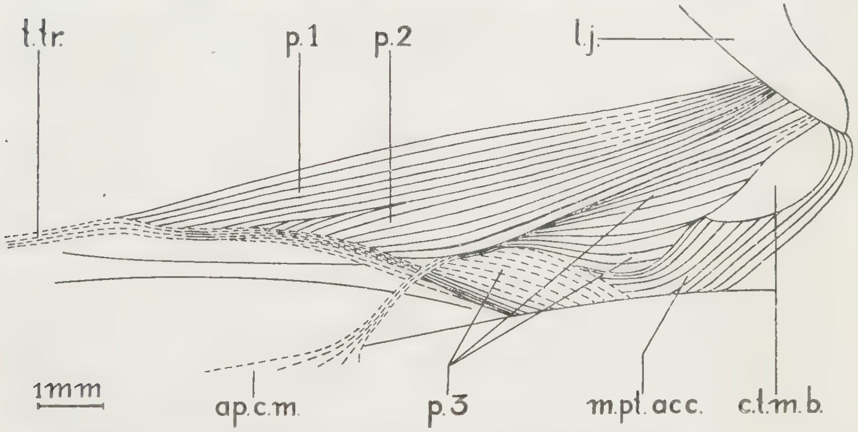


Fig. 16. Dorso-lateral view of the musculus adductor mandibulae internus pterygoideus. The lower jaw is bent upwards. *ap.c.m.*, aponeurosis to the connective tissue of the mouth; *c.t.m.b.*, connective tissue of the bottom of the mouth; *l.j.*, lower jaw; *m.pt.acc.*, musculus adductor mandibulae internus pterygoideus accessorius; *p. 1, 2, 3*, part 1, 2, 3 of the muscle; *t.tr.*, tendon attached to the transversum.

The third part *(p. 3)* starts with an aponeurosis *(ap.c.m.)* in the connective tissue of the corner of the mouth. Caudalwards it broadens and continues in a strong muscular bundle, running to the flat ventral plane of the lower jaw. The broadened part of the aponeurosis has a loose connection with the aponeurosis of the second part.

The fourth part *(m.pt.acc.)* is often called musculus pterygoideus accessorius (Haas, 1930, a.o.) and runs from the caudo-lateral part of the pterygoid. It is attached to the medial plane of the lower jaw, but more caudally than the third part.

The four parts distinguished rostrally are unequally split up over the three bundles attached to the lower jaw.

7. *Musculus levator pterygoidei* (figs 1, 2 and 5; *m.l.pt.*)

This muscle runs from the region of the cerebral skull caudal to the orbita to the dorsal plane of the pterygoid.

The place of attachment on the cerebral skull lies just ventro-caudal to and under the base of the processus postorbitalis *(p.p.o.)*. It is not sharply demarcated, especially the ventral and caudal border are not exactly determinable.

The fibres are attached musculously with very sharp angles and in the lateral part of the area of attachment they only glide over the skull and are connected to it with loose connective tissue.

The place of attachment on the pterygoid lies around and caudal to the articulation with the transversum. A detailed description of the places of attachment to the pterygoid is given at the musculus protractor pterygoidei.

The way of attachment to the pterygoid is musculous.

The muscle fibres are running straight from one place of attachment to the other. The rostral fibres are shorter than the caudal ones.

8. *Musculus protractor pterygoidei* (figs 2 and 5; *m.p.pt.*)

This muscle runs from the ventral surface of the cerebral skull to the dorsal plane of the caudal part of the pterygoid.

The place of attachment on the cerebral skull lies on the ventral surface caudal to the orbita and has an almost triangular shape. The angles of the rhomb-shaped area of the parasphenoid *(p.sph.)* lie in the median of the basis cranii and in the caudo-ventral corners of the orbitae. From the lateral angle runs a costa *(co. p.sph.)* straight medio-caudally to a point at a short distance from the sutura *(s.sph.)* between para- and basisphenoid. The caudal part of this costa lies in the median, where the costae of both sides coincide. From the lateral angle runs also a crista *(cr.p.sph.)* into a latero-caudal direction on the latero-ventral surface.

Between this crista *(cr.p.sph.)* at one side and the costa *(co.p.sph.)* at the other side lies the triangular area of attachment of the musculus protractor pterygoidei. The caudal border of this triangular area runs medio-laterally and is not specially indicated. Its medial end starts just caudal to the caudal angle of the rhomb-shaped area.

The places of attachment of the left and right musculus protractor pterygoidei don't meet each other in the median, but are separated by the medial part of the costa *(co.p.sph.)*.

The place of attachment is a shallow fossa.

The attachment is musculous to the whole area.

The pterygoid *(pt.)* is a long bone, wave-shaped in a transverse section. The medial part of the pterygoid is directed medio-dorsally. The lateral part is directed laterally, a little dorsally. The margin is bent ventralwards. Thus two grooves can be distinguished. The medial one, between the medial and the lateral part, is facing dorsalwards. The second, formed by the lateral part and its margin, is facing ventralwards. The pterygoid has its greatest breadth at about 2 mm from its caudal end. Near the articulation with the transversum the grooves diminish gradually and the pterygoid becomes ellipsoid in a transverse section.

The musculi levator and protractor pterygoidei are musculously attached to the first groove. To the second groove is attached the musculus adductor mandibulae internus pterygoideus accessorius, described above.

The muscle fibres run parallel from one place of attachment to the other.

9. *Musculus protractor quadrati* (figs 2, 8 and 17; *m.p.q.*)

This muscle runs from the ventral surface of the cerebral skull to the quadratum into a caudo-dorsal direction.

The place of attachment on the cerebral skull lies on the transverse crista on the basisphenoid *(cr.b.sph.)*. It extends from the base of the spina *(sp.b.sph.)* of this crista *(cr.b.sph.)* nearly to the processus caudolateralis *(pr.c.l.)*.

The attachment occurs by a short aponeurosis.

The area of attachment on the quadratum lies medial to the area of attachment of the musculus adductor mandibulae externus posterior, between this area and the crista *(cr.q.)*. The area is narrow and reaches from the articulation with the lower jaw to about halfway the small rostral crista *(cr.q.)* on the quadratum.

The muscle is musculously attached to this area.

The muscle bundle is flat.

10. *Musculus retractor vomeris* (figs 1, 2, 4 and 17; *m.r.v.*)

This muscle runs from the most ventro-caudal point of the vomer *(v.)* to the cerebral skull.

The palatinum is rostrally connected with the vomer *(v.)* and with the maxillare by strong connective tissue. Medial to the palatinum the vomer bears a short conical extension. On this extension is attached a little tendon *(t.m.r.v.)*, to which the muscle fibres are attached.

The place of attachment to the cerebral skull is the rostral part of a small, rather deep groove *(gr.l.)*. This groove lies close and lateral to the triangular place of attachment of the musculus protractor pterygoidei. The place of attachment is a triangular area, situated in the caudoventral corner of the orbita. The attachment is musculous.

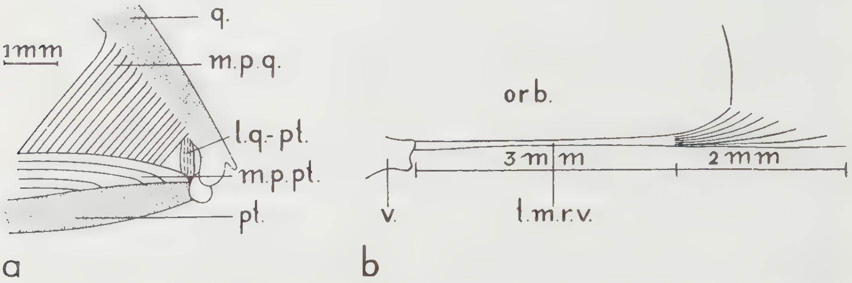


Fig. 17. a. Lateral view of the musculus protractor quadrati. b. Lateral view of the musculus retractor vomeris. *l.q.-pt.*, ligamentum quadrato-pterygoidale; *m.p.pt.*, musculus protractor pterygoidei; *m.p.q.*, musculus protractor quadrati; *orb.*, orbita; *pt.*, pterygoid; *q.*, quadratum; *t.m.r.v.*, tendon of the musculus retractor vomeris to the vomer; *v.*, vomer.

The fibres diverge from the tendon to the cerebral skull.

11. *Musculus retractor palatini* (figs 1, 2 and 5; *m.r.p.*)

This muscle runs from the ventral surface of the cerebral skull to the palatinum *(pal.)*.

The place of attachment on the cerebral skull lies just caudal to the place of attachment of the musculus retractor vomeris *(m.r.v.)* in an shallow continuation of the groove (*gr.l.*). This groove runs from the orbita to the foramen pro nervo V^2 between the spherical lateral wall of the cerebral skull and the crista of the parasphenoid *(cr.p.sph.)*. The area of attachment is narrow and rather short. This area is not clearly outlined.

The attachment is musculous.

The place of attachment on the palatinum lies on the narrow caudodorsal side. In some cases it extends a short distance on both sides and on the rostro-dorsal side of the pterygoid.

The attachment is musculous.

The fibres run parallel into a ventro-rostral direction.

12. *Musculus retractor quadrati* (fig. 7; *m.r.q.*)

This muscle runs from the caudo-dorsal point of the quadratum to the cervical region into a caudo-ventral direction.

Close to the low crista *(cr.q.d.)* and ventral to it the quadratum bears a little crista. To this little crista is the musculus retractor quadrati tendinously attached. The description of an attachment to the supratemporale, given by WOLTER (1924), is not right. His argument against KATHARINER (1900) and HAGER (1906) does not hold good.

In the cervical region the muscle is aponeurotically attached to the skin.

The muscle, included the tendon, has the same length as the quadratum.

13. *Musculus depressor mandibulae* (figs 3, 7, 10, 11 and 13; *m.d.m.*)

This muscle runs from the quadratum and the dorsal surface of the cerebral skull to the lower jaw.

The quadratum is a long flat bone, a little broadened and flattened at the dorsal part. This dorsal part is divided by a shallow nick *(sh.n.)*. Close to the dorsal border and ventral to it lies a low crista *(cr.q.d.)* on the lateral surface of the quadratum. This low crista forms the dorsal border of the place of attachment of the musculus depressor mandibulae. The ventral border of the place of attachment is rather variable. It lies about 1 mm dorsal to the ventral border of the quadratum-body. This ventral border of the place of attachment may be determined by the extension of the cartilaginous capsule around the articular knobs.

The muscle is musculously attached to the whole area.

The place of attachment on the cerebral skull lies on a crista *(cr.p.)*, running transversely on the roof between the supratemporalia. It occupies a very short medial part of the crista *(cr.p.)*. The attachment is aponeurotic.

The place of attachment on the lower jaw lies caudal to the articulation with the quadratum, on the processus retro-articularis *(pr.r.-a.)*. The processus retro-articularis bends caudally a little medialwards. Its dorsal plane is almost quadrangular, the long sides are curved inwards. The surface is a little sloping medialwards. The caudal plane stands perpendicularly on the longitudinal axis of the lower jaw. This caudal plane has the shape of a rounded quadrangle. In its dorso-medial corner lies the foramen pro nervo faciale.

The muscle fibres are musculously attached to the whole dorsal and caudal plane of the processus retro-articularis.

The muscle is indistinctly divided into two parts. The rostral part runs from the quadratum to the dorsal, and partly to the caudal plane of the processus retro-articularis. The caudal part runs from the cerebral skull to the caudal plane of the processus retro-articularis. This caudal part is attached to the cerebral skull by a relatively long tendon. In one case the tendon was very short and the caudal bundle was a little broader.

14. *Musculus cervico-mandibularis* (figs 7, 14 and 18; *m.c.-m.*)

This muscle runs into a caudo-dorsal direction from the most ventro-lateral point of the quadratum to the most dorsal part of the cervical region.

The quadratum bears two knobs for the articulation with the lower jaw. The lateral knob *(l.kn.)* is almost spherical, whereas the medial one *(m.kn.)* is a little flattened in a parasagittal plane. The most lateral point of the lateral knob serves for the attachment of a short aponeurosis *(ap.m.c.-m.)*. The place of attachment of the aponeurosis is not sharply determinable, because of the tangential way of attachment and the continuation of the aponeurosis in the ligamentum quadrato-maxillare *(l.q.-m.)*, which runs to the glandula venenata. An attachment of this muscle to the processus postglenoidalis of the lower jaw, as Haas (1931) mentions for other Viperidae, does not exist.

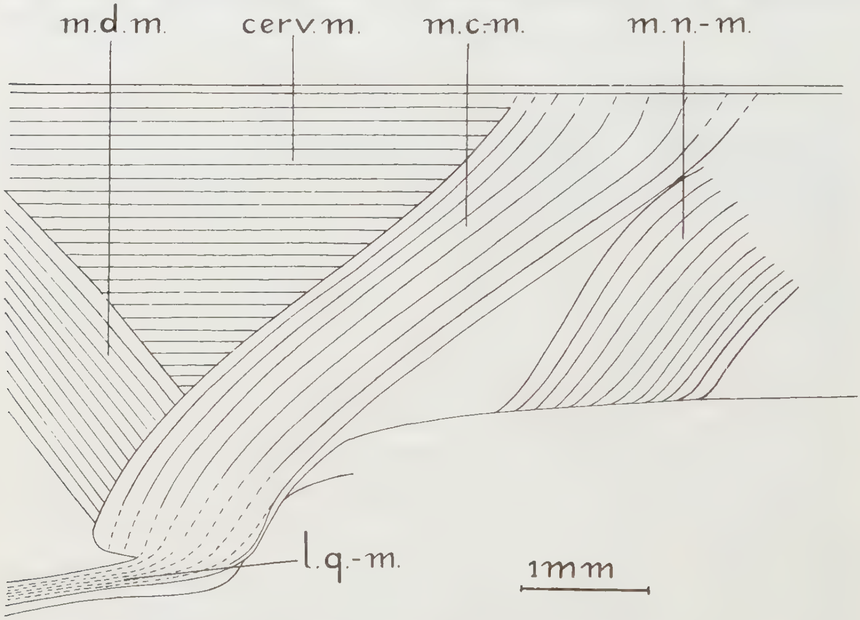


Fig. 18. Lateral view of the left musculus cervico-mandibularis. *cerv.m.*, cervical muscles; *l.q.-m.*, ligamentum quadrato-maxillare; *m.c.-m.*, musculus cervico-mandibularis; *m.d.m.*, musculus depressor mandibulae; *m.n.-m.*, musculus neuro-mandibularis.

The attachment to the cervical region lies dorsal to the fifth–seventh vertebrae.

The muscle is aponeurotically attached to the connective tissue connecting the processus spinosi dorsales.

The muscle fibres run parallel from one place of attachment to the other, only in the cervical region they diverge a little. The bundle is about 7–10 mm long, 2–3 mm broad and some fibres thick and it makes an angle of 45° with the medial plane.

15. *Musculus neuro-mandibularis* (figs 11, 19 and 20; *m.n.-m.*)

This muscle runs from the lower jaw to the dorsal part of the cervical region.

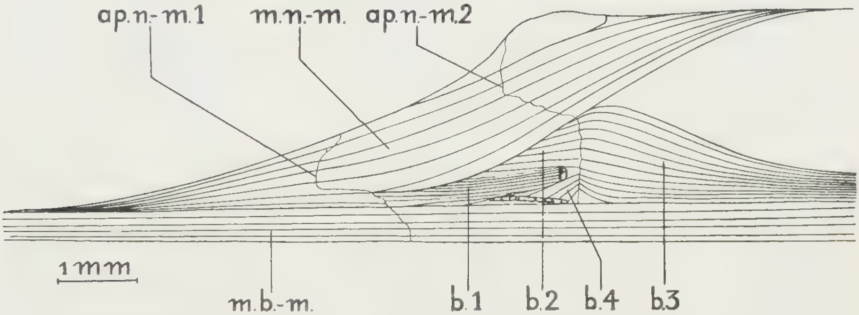


Fig. 19. Lateral view of the left musculus neuro-mandibularis. *ap.n.-m. 1, 2*, transverse aponeurosis of the musculus neuro-mandibularis 1, 2; *b. 1, 2, 3, 4*, bundle 1, 2, 3, 4 of the mentioned muscle; *m.b.-m.*, musculus branchio-mandibularis; *m.n.-m.*, musculus neuro-mandibularis.

The place of attachment on the lower jaw lies on the ventral ridge of the dentale. The place of attachment is very narrow. It extends from a point ventral to the third tooth to the most caudal point of the dentale.

The attachment is aponeurotic by a strong tangential aponeurosis continuing on the lateral surface of the periost and strongly connected with it. The remaining part of this aponeurosis is part of the musculus branchio-mandibularis *(m.b.-m.)* and the musculus mylohyoideus *(m.myl.)*.

The place of attachment in the cervical region lies in the median dorsal to the 6th–7th vertebrae. It is a small narrow area on the connective tissue covering the cervical muscles.

The attachment is musculous and occurs at very acute angles. The muscle is rather long, broad and thin. It is divided into three parts by two transverse aponeuroses. The first aponeurosis *(ap.n.-m.1)* lies rostroventrally at a short distance from the articulation of the lower jaw. The aponeurosis continues in the musculus branchio-mandibularis *(m.b.-m.)*.

The muscle branches off two bundles from this aponeurosis: a small one *(b.1)*, lying laterally and running caudalwards to the skin, and a second broader one *(b.2)*, lying medially, which runs to the second aponeurosis.

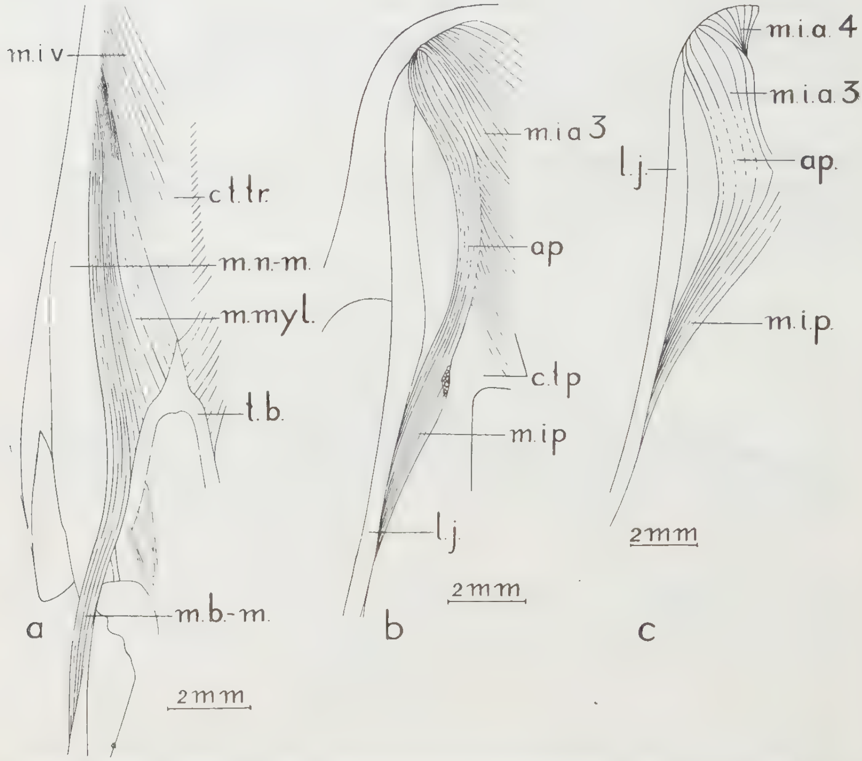


Fig. 20. Ventral view of the left intermandibularis muscular system. a, ventral layer; b, ventral layer and a part of the musculus intermandibularis posterior removed; c, a part of the musculus intermandibularis anterior 3 removed. *ap.*, aponeurosis; *c.t.p.*, connective tissue plate in the bottom of the mouth; *c.t.tr.*, connective tissue sheath round the trachea; *l.j.*, lower jaw; *m.b.-m.*, musculus branchio-mandibularis; *m.i.a.3*, musculus intermandibularis anterior 3; *m.i.a.4*, musculus intermandibularis anterior 4; *m.i.p.*, musculus intermandibularis posterior; *m.i.v.*, musculus intermandibularis ventralis; *m.myl.*, musculus mylohyoideus; *m.n.-m.*, musculus neuro-mandibularis; *t.b.*, tongue-bone.

This second aponeurosis *(ap. n.-m.2)* lies close to the articulation and ventral to it. From this aponeurosis start some fibres *(b.4)* into a rostroventral direction to the connective tissue wall of the pharynx.

A third, broad bundle *(b.3)* starts from this aponeurosis into a caudal direction and ends in a cervical muscle on the same level as the 8th vertebra.

16. *Musculus branchio-mandibularis* (figs 11 and 20; *m.b.-m.*)

This muscle runs from the lower jaw to the ventro-lateral side of the body, on the level of the 5th–6th rib. It runs almost parallel with the musculus neuro-mandibularis *(m.n.-m.)* and joins this muscle on its ventro-medial side.

The attachment to the lower jaw occurs by means of the common aponeurosis described at the musculus neuro-mandibularis, just rostral to the place of attachment of that muscle.

The place of attachment on the ventral side of the body lies on the connective tissue covering the muscles between the ribs. The demarcation of this area is unsharp and very variable.

The attachment is musculous.

The muscle fibres run parallel. The muscle is long, broad and flat and divided into two parts by the first transverse aponeurosis *(ap.n.-m. 1)* described above.

17. *Musculus mylohyoideus* (figs 11 and 20; *m.myl.*)

This muscle runs from the lower jaw to the tongue-bone.

The attachment to the lower jaw occurs by means of the common aponeurosis described at the musculus neuro-mandibularis, rostral to the place of attachment of the musculus branchio-mandibularis.

The attachment to the tongue-bone *(t.b.)* occurs by means of the perichondrium.

The muscle runs parallel with the musculus branchio-mandibularis, and that rostro-medial to it. It cannot clearly be distinguished from the musculus branchio-mandibularis *(m.b.-m.)* and the musculus intermandibularis ventralis *(m.i.v.)*.

In some cases the bundle could be separated into three parallel bundles, lying close together. It is possible that this separation may be caused by the different angles at which the muscle fibres are attached.

In one specimen a superficial part of the fibres of the musculus mylohyoideus ran on ventral to the tongue-bone. The fibres from both sides met each other in the median.

18. *Musculus intermandibularis* (figs 10, 11 and 20; *m.i.a.3*, *m.i.a.4*, *m.i.p.*, *m.i.v.*)

This muscle consists of four bundles, running into different directions and attached to different places.

The first part is the musculus intermandibularis ventralis *(m.i.v.)*, which runs from the lower jaw to the connective tissue in the median line ventral to the trachea.

The attachment to the lower jaw occurs by means of the aponeurosis described at the musculus neuro-mandibularis.

The connective tissue in the median is connected with the trachea.

The muscle fibres run into a caudo-medial direction. Rostralwards the amount of muscle fibres diminishes to the place where only the connective tissue remains.

The muscle lies rostral to the musculus mylohyoideus and cannot clearly be distinguished from it. Many authors (HOFFMANN, 1890; LUBOSCH, 1933) describe both muscles as a single one.

The second part is the musculus intermandibularis posterior *(m.i.p.)*, which runs from the lower jaw to the median line into a rostro-medial direction.

The place of attachment on the lower jaw lies about halfway the length on the medio-ventral surface; it is a small oval spot without sharp demarcations.

The way of attachment is musculous and occurs at acute angles.

The place of attachment in the median lies on a connective tissue plate *(c.t.p.)*, forming a sheath round the tongue and connected with the tongue-bone.

In some cases the fibres of the muscles from both sides meet each other in the median. Sometimes the muscle ends in an aponeurosis connected with the third part of the musculus intermandibularis (*m.i.a.3*)

The third and the fourth part together form the musculus intermandibularis anterior. The third part (*m.i.a.3*) runs from the most rostral point on the latero-ventral plane of the lower jaw caudalwards to the median.

The most rostral part of the lower jaw is bent inwards. The place of attachment lies partly on the lateral surface of the lower jaw, partly on a connective tissue plate lying ventral to the fourth part. This connective tissue plate is connected with the ligamentum intermandibulare and forms a part of the bottom of the mouth. The attachment to the lower jaw is not sharply demarcated, because of the tangential connection with the periost. The attachment to the connective tissue may be considered as an aponeurotic one. The fibres run caudally, almost parallel to the rostral part of the lower jaw.

The place of attachment in the median lies on the connective tissue plate connected with the trachea. This plate is extended from a point some mm caudal to the ligamentum intermandibulare, to a point dorsal to the place of attachment of the second part, by which it is ventrally a little covered and hardly to be separated from it. The attachment is very loose. Both parts are connected by the aponeurosis described at the second part.

The fibres of the third part start almost in one point, diverge strongly caudalwards and then run parallel caudally. Consequently the medial fibres run with a little bow into a direction from lateral to medial, whereas the lateral fibres run almost straight caudalwards.

The fourth part *(m.i.a.4)* runs from the lower jaw and the ligamentum intermandibulare to the median.

The place of attachment on the lower jaw lies on the narrow ventrorostral surface. The attachment is musculous.

The place of attachment in the median is almost point-shaped, and lies about 2 mm caudal to the ligamentum intermandibulare. The fibres converge strongly and form a narrow bundle, which covers the glandula submaxillaris ventrally.

19. *Musculus genio-hyoideus* (figs 11 and 21; *m.g.-h.*)

This muscle runs from the lower jaw to the connective tissue around the musculus hyoglossus.

The place of attachment to the lower jaw lies just dorso-medial to the place of attachment on the third part of the musculus intermandibularis on the medial plane of the lower jaw. The area lies close to the ventral border of the jaw and shows no special demarcations on the bone. The attachment is musculous.

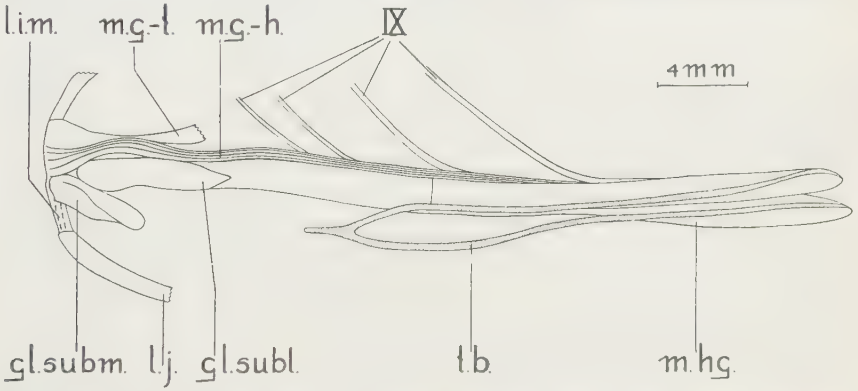


Fig. 21. Ventral view of the tongue. *gl.subl.*, glandula sublingualis; *gl.subm.*, glandula submaxillaris; *l.i.m.*, ligamentum intermandibulare; *l.j.*, lower jaw; *m.g.-h.*, musculus genio-hyoideus; *m.g.-t.*, musculus genio-trachealis; *m.hg.*, musculus hyoglossus; *t.b.*, tongue-bone; *IX*, nervus glossopharyngeus.

The very long and thin muscle runs straight caudalwards to the connective tissue around the musculus hyoglossus *(m.hg.)* and cannot macroscopically be distinguished from this connective tissue. The attachment may be considered a musculous one.

20. *Musculus genio-trachealis* (figs 11 and 22; *m.g.-t.*)

This muscle runs from the lower jaw to the trachea.

The place of attachment on the lower jaw lies just caudal to the place of attachment of the musculus genio-hyoideus. It is a small narrow area without any clear demarcations on the bone. The attachment is musculous.

The place of attachment to the trachea is a small area on the lateral side of the 3rd–6th tracheal cartilaginous rings. The attachment is musculous.

The fibres of this small thin muscle run straight from one place of attachment to the other.

21. *Musculus tracheo-hyoideus* (fig. 22; *m.t.-h.*)

This muscle runs from the bottom of the mouth and the connective tissue medial to the musculous branchio-mandibularis to the trachea. The attachment to the trachea occurs musculously to the first and the second cartilaginous ring, close and rostro-dorsal to the place of attachment of the musculus genio-trachealis.

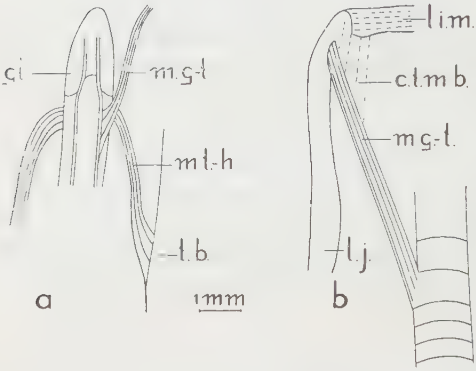


Fig. 22. Ventral view of the muscles to the trachea. a, musculus genio-trachealis; b, musculus tracheo-hyoideus, *c.t.m.b.*, connective tissue in the bottom of the mouth; *gl.*, glottis; *l.i.m.*, ligamentum intermandibulare; *l.j.*, lower jaw; *m.g.-t.*, musculus genio-trachealis; *m.t.-h.*, musculus tracheo-hyoideus; *t.b.*, tongue-bone.

22. *Musculus hyoglossus* (fig. 21; *m.hg.*)

The tongue is about 4 cm long, *i.e.* twice the length of the skull. The tongue consists of the paired musculus hyoglossus over the whole length. For the greater part the muscles of both sides are connected by a strong tissue covering the muscle. The rostral part is free and forms the bifurcated tongue of the snake. The most caudal parts are also free from each other and are both connected with a horn of the tongue-bone. The whole caudal half is laterally covered by the musculus genio-hyoideus (*m.g.-h.*)

The whole musculus hyoglossus and the tongue-bone lie in a connective tissue sheet.

23. *Musculus spinalis capitis* (figs 3 and 23; *m.s.c.*)

This muscle runs from the supraoccipitale to the cervical region dorsal to the fifth up to and including the thirteenth vertebra.

The dorsal surface of the occipital region lies on a more ventral level than that of the remaining cerebral skull. This surface of the occipital region has an almost triangular shape. The basal side of this triangle is formed by the straight, sharp, caudal edges of the exoccipitalia. The other sides, which run from caudo-lateral to rostro-medial are formed by cristae *(cr.o.)* on the exoccipitale and the supraoccipitale. The top of the triangle reaches the superficial demarcation between the parietale and the supraoccipitale in the median. Many times the standing sides of the triangle are a little lobed, in that way that the two caudal lobes are of the same length and the rostral one has about half this length. The shape of the sides, however, is very variable in this respect. The basal angles of the triangle are invaginated.

The attachment of the musculus spinalis capitis occurs aponeurotically to the rostral lobe of the crista *(cr.o.)*.

The muscle fibres start from the ventral plane of the aponeurosis. The attachment in the cervical region occurs partly to the most rostral tendon of the musculus spinalis, partly to the connective tissue between the processus spinosi dorsales *(pr.sp.d.)*. The connective tissue between these processus cannot macroscopically be distinguished from the tendines and fasciae of the musculus spinalis.

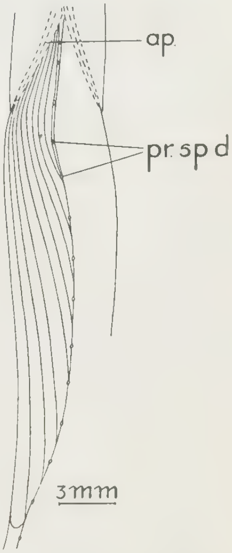


Fig. 23. Dorsal view of the musculus spinalis capitis. *ap.*, aponeurosis; *pr.sp.d.*, processus spinosus dorsalis.

24. *Musculus longissimus capitis* (fig. 3; *m.l.c.*)

This muscle runs from the supraoccipitale and the exoccipitale to the caudal region of the body.

The attachment to the occipitalia occurs aponeurotically to the rostral and partly to the caudal lobe of the crista *(cr.o.)*, mentioned above. The muscle fibres start from the ventral plane of the aponeurosis. The muscle runs on straight to the cauda. The fascia of the muscle is connected with the dorsal surface of the vertebrae, same as the fascia of the other dorsal muscles.

25. *Musculus ilio-costalis occipitalis* (fig. 3; *m.i.-co.o.*)

This muscle runs from the exoccipitale to the cauda.

The place of attachment on the exoccipitale lies on the caudo-lateral part of the crista (*cr.o.*).

The attachment is aponeurotic. The muscle fibres start from the ventral plane of the aponeurosis and run a little medio-dorsalwards. They run on as far as the cauda, dorsally along the processus transversi and laterally along the processus spinosi dorsales.

26. *Musculus rectus capitis dorsalis* (fig. 3; *m.r.c.d.*)

This muscle runs from the occiput to the second vertebra.

The place of attachment on the occiput lies on the flat triangular area caudal to the lobed crista *(cr.o.)*. A narrow part of this area, just caudal to the crista *(cr.o.)*, is facing caudally. The place of attachment occupies this part caudal to the first and second lobe in the crista (*cr.o.*).

The attachment is musculous.

The area of attachment to the second vertebra is almost point-shaped. It lies on the latero-dorsal side of the processus spinosus dorsalis.

The attachment is musculous.

The muscle fibres converge from the occiput towards the second vertebra. Rostrally there is much loose connective tissue between the fibres.

27. *Musculus obliquus capitis* (fig. 3; *m.o.c.*)

This muscle runs from the occiput to the third and fourth vertebra.

The place of attachment on the occiput lies on the part facing caudally and extends from the area of attachment of the musculus rectus capitis dorsalis to the latero-caudal corner of the dorsal surface of the cerebral skull. There exists no sharp demarcation between the place of attachment of this muscle and that of the forementioned one.

The attachment is musculous.

The places of attachment in the cervical region lie on the lateral surfaces of the processus spinosi dorsales of the third and fourth vertebra.

The attachment is musculous.

The fibres run parallel from the occiput into a caudo-medial direction. In the cervical region the fibres of the musculus obliquus cervicis, starting from the vertebrae, join the fibres of the musculus obliquus capitis and constitute the whole musculus obliquus.

28. *Musculus longissimus colli lateralis* (figs 2 and 24; *m.l.c.l.*)

This muscle runs from the occiput caudalwards through the whole body.

The place of attachment lies on the most lateral processus *(pr.c.l.)* of the transverse crista *(cr.b.sph.)* on the basisphenoid. The place of attachment lies between the place of attachment of the aponeurosis of the musculus rectus capitis ventralis minor *(m.r.c.v.mi.)* and that of the aponeurosis of the musculus ilio-costalis occipitalis *(m.i.-co.o.)*.

The attachment is aponeurotic. The fibres start from the dorsal surface of the aponeurosis and run on along the latero-dorsal side of the body.

29. *Musculus rectus capitis ventralis major* (figs 2 and 24; *m.r.c.v.ma.*)

This muscle runs from the ventral spina *(sp.b.sph.)* on the basisphenoid to the hypapophyses of the first to and including the tenth vertebra.

The muscle is aponeurotically attached to the spina *(sp.b.sph.)*.

The attachment in the cervical region occurs principally to the connective tissue between the hypapophyses. Every hypapophysis is connected with the next one by a paired band of connective tissue, lying paramedially. The band is extended up to the vertebral body. The muscle is for the greater part musculously attached to the hypapophysis, but also to the connective tissue.

The fibres run almost straight from one place of attachment to the other, which consequently shows the fibres that are attached more rostrally as the shorter ones.

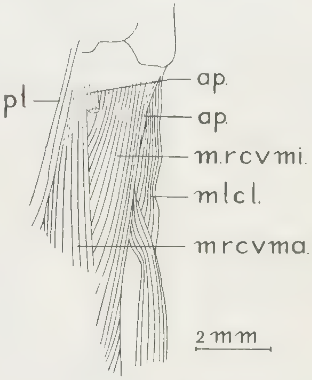


Fig. 24. Ventral view of the ventral cervical muscles. The right musculus rectus capitis ventralis major removed. *ap.*, aponeurosis; *m.l.c.l.*, musculus longissimus colli lateralis; *m.r.c.v.ma.*, musculus rectus capitis ventralis major; *m.r.c.v.mi.*, musculus rectus capitis ventralis minor; *pt.*, pterygoid.

30. *Musculus rectus capitis ventralis minor* (figs 2 and 24; *m.r.c.v.mi.*)

This muscle runs from the occiput to the cervical region, from the first to and including the fifth vertebra. Sometimes the muscle cannot clearly be distinguished from the musculus rectus capitis ventralis major.

The rostral border of the place of attachment on the occiput is the crista on the basisphenoid *(cr.b.sph.)* mentioned above. The caudal border is formed by the foramen magnum. Laterally the place of attachment ends on the medial basal part of the processus caudo-lateralis *(pr.c.l.)*. Medially it reaches the median. The place of attachment on the occiput is facing caudo-ventrally.

The attachment is musculous, except that to the processus caudolateralis, which is aponeurotic.

The place of attachment to the vertebrae lies just dorsal to the musculus rectus capitis ventralis major, on the hypapophyses and the connective tissue between these processus. The attachment occurs from the first up to and including the fifth vertebra. On the first and the second vertebra the attachment reaches the pleurapophysis.

It must be observed that the musculus rectus capitis ventralis minor as well as the musculus rectus capitis ventralis major consist of flat bundles, which are only attached to the most ventro-lateral parts of the hypapophyses. The space between the lateral plane of the hypapophysis and the parapophysis is occupied by the musculus longus colli, which does not reach the epistropheus, but starts at the third vertebra.

The same space at the atlas and the epistropheus is occupied by the musculus rectus capitis ventralis minor.

C. THE LIGAMENTS

1. *Ligamentum quadrato-maxillare* (figs 1, 8, 14, 18, 25 and 26; *l.q.-m.*)

This ligamentum runs from the latero-ventral knob of the quadratum to the maxillare.

The place of attachment on the quadratum lies on the most lateral point of the latero-ventral knob that serves as the articulation with the lower jaw. The ligamentum cannot clearly be distinguished from the aponeurosis of the musculus cervico-mandibularis (figs 14 and 18) and though it is a tangential attachment, it is yet a very firm one.

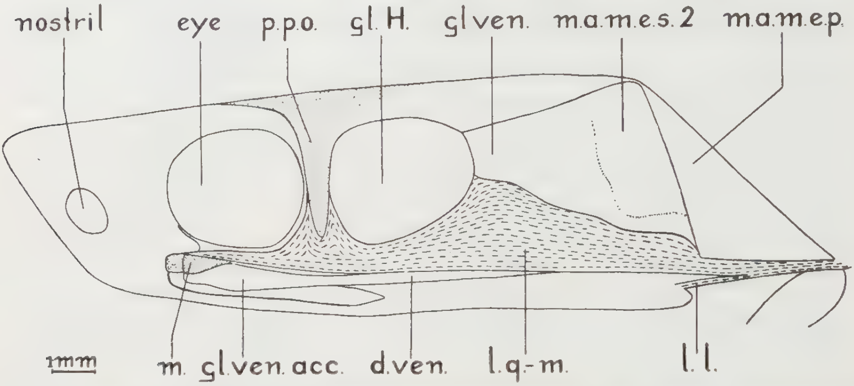


Fig. 25. Lateral view of the left ligamentum quadrato-maxillare in situ. *d.ven.*, ductus venenatus; *gl.H.*, glandula Harderiana; *gl.ven.*, glandula venenata; *gl.ven.acc.*, glandula venenata accessoria; *l.l.*, ligamentum to the corner of the mouth; *l.q.-m.*, ligamentum quadrato-maxillare; *m.*, maxillare; *m.a.m.e.p.*, musculus adductor mandibulae externus profundus; *m.a.m.e.s.2*, musculus adductor mandibulae externus superficialis 2; *p.p.o.*, processus postorbitalis.

The ligamentum runs rostralwards, where it is connected with the connective tissue around the glandula venenata *(gl.ven.)*.

Before reaching the bag of the glandula, it branches off a part which runs to the corner of the mouth: the ligamentum laterale (fig. 25; *l.l.*) (Wolter, 1924).

The ventral part of this bag can be distinguished from the continuation of the ligamentum by the firmer and glittering tissue of that ligamentum. The rostral end of the ligamentum, running rostral to the glandula Harderiana *(gl.H.)*, reaches the processus postorbitalis *(p.p.o.)* at its ventral point. It is broadened when extending around this point, fades into the periost and continues much narrower rostralwards.

The ligamentum is firmly attached to the maxillare to one point mainly, the most rostro-lateral point. The attachment to the lateral plane of the maxillare is weaker and tangential.

The most rostral part of the ligamentum, running from the processus postorbitalis to the maxillare, is often called ligamentum orbitale (HAAS, 1930).

2. *Ligamentum supratemporale-glandulare* (figs 9 and 14; *l.s.-gl.*)

This ligamentum runs from the lateral ridge of the supratemporale to the connective tissue bag of the glandula venenata.

The flat supratemporale bears on its crista-like lateral ridge a pointshaped processus *(pr.s.t.)* at a short distance from its caudal end. This processus forms the rostral border of the articulation with the quadratum. The ligamentum is attached to the ventro-rostral ridge of the processus.

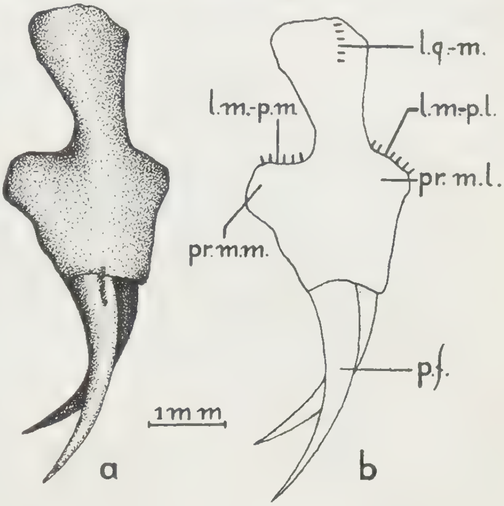


Fig. 26. Rostral view of the left maxillare. a, drawn from nature; b, diagram. *l.m.-p.l.*, ligamentum maxillo-praefrontale laterale; *l.m.-p.m.*, ligamentum maxillo-praefrontale mediale; *l.q.-m.*, ligamentum quadrato-maxillare; *p.f.*, poison-fang; *pr.m.l.*, processus maxillaris lateralis; *pr.m.m.*, processus maxillaris medialis.

The attachment of the ligamentum cannot macroscopically be distinguished from the capsule of the articulation between the supratemporale and the quadratum.

Rostralwards the ligamentum is broadened and medially connected with the most dorso-caudal part of the bag around the glandula venenata. The fibres of the ligamentum diverge into the connective tissue of the bag.

3. *Ligamentum quadrato-pterygoidale* (figs 5, 8 and 17; *l.q.-pt.*)

This ligamentum runs from the distal part of the quadratum to the caudo-dorsal part of the pterygoid.

The place of attachment on the quadratum lies between the cartilage surrounding the medial articular knob *(m.kn.)*, and the place of attachment of the musculus protactor quadrati *(m.p.q.)*. The ligamentum is short and runs straight ventrally to the dorsal plane of the pterygoid. Here it is attached to a spot between the place of attachment of the musculus protractor pterygoidei and the cartilage surrounding the articular knob of the pterygoid.

The ligamentum is hardly to be distinguished from the cartilage of that articular knob, nor from that of the articular knob of the quadratum.

4. *Ligamentum parieto-supratemporale* (figs 3 and 9; *l.p.-s.*)

This ligamentum runs from the latero-caudal part of the parietale to the medial ridge of the supratemporale.

The supratemporale *(s.t.)* lies in a triangular groove *(gr.)*, as described above. This groove is medially bordered by a crista *(cr.p.)* of the parietale, running from rostro-lateral to caudo-medial. At a short distance from the place of attachment of the cervical muscles (description see above) the crista *(cr.p.)* turns medialwards. The place of attachment of the ligament lies on this crista *(cr.p.)* from the articular surface of the supratemporale to close to the median.

The supratemporale is a long flat bone (description above). The ligamentum is attached to the whole crista-like medial ridge.

The rostral part of the ligamentum is very short, whereas the caudal part is lengthened and has a triangular shape, as a consequence of the great distance between the caudally extending part of the supratemporale and the parietal crista *(cr.p.)*.

5. *Ligamentum maxillo-praefrontale laterale* (figs 1, 26 and 27; *l.m.-p.l.*)

This ligamentum runs from the latero-caudal ridge of the maxillare to the latero-caudal ridge of the praefrontale.

The maxillare is a triangular prismatic bone, of which the lateral and the medial rib are invaginated about halfway the longitudinal axis. Ventral to these invaginations the maxillare is somewhat broadened in a latero-medial direction, so that each of the two ribs bears a processus. The processus on the lateral rib *(pr.m.l.)* has a triangular shape.

The ligamentum is attached to the dorsal crista-like ridge of this triangular processus of the lateral rib *(pr.m.l.)*. The praefrontale is an almost circular bone in a caudal view. It is more or less disk-shaped, so that the lateral face has a caudal as well as a rostral crista-like ridge *(cr.pf.c.* resp. *cr.pf.r.)*.

The ligamentum is attached to the whole caudal crista-like ridge (*cr.pf.c.*) of the lateral face. It is a thin band of the same breadth all over the length.

6. *Ligamentum maxillo-praefrontale mediale* (figs 26 and 28; *l.m.-p.m.*)

This ligamentum runs from the medio-caudal ridge of the maxillare to the ventral ridge of the praefrontale.

The medial rib of the maxillare shows a quadrangular processus *(pr.m.m.)*. The ligamentum is attached to the dorsal crista-like ridge of this quadrangular processus.

In a caudal view the praefrontale is a circular bone (see above), of which the ventral side is somewhat straightened. In a parasagittal section this ventral part of the praefrontale has a triangular shape.

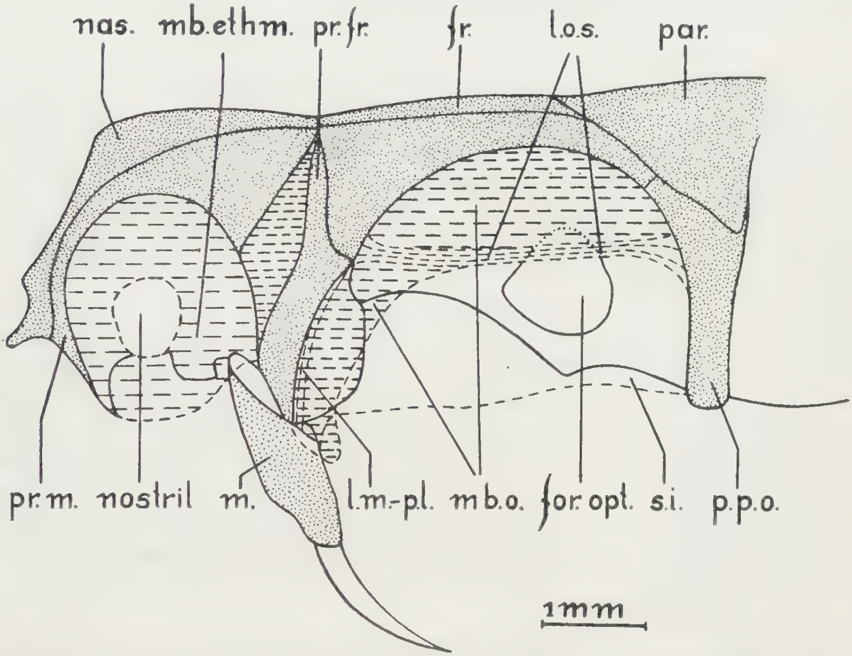


Fig. 27. Lateral view of the membranes and ligaments in the left olfactorial and orbital region. *fr.*, frontale; *for.opt.*, foramen opticum; *l.m.-p.l.*, ligamentum maxillo-praefrontale laterale; *l.o.s.*, ligamentum orbitale superior; *m.*, maxillare; *mb.ethm.*, membrana ethmoidalis; *mb.o.*, membrana orbitalis; *nas.*, nasale; *par.*, parietale; *p.p.o.*, processus postorbitalis; *pr.fr.*, praefrontale; *pr.m.*, praemaxillare; *s.i.*, septum interorbitale.

The ligamentum is attached to the medial half of the ventral ridge of this ventral part.

7. *Ligamentum orbitale superius* (fig. 27; *l.o.s.*)

This ligamentum runs from the latero-caudal ridge of the praefrontale and the lateral ridge of the frontale to the rostral ridge of the processus postorbitalis in the orbita.

On the latero-caudal ridge the praefrontale bears a small spina on the spot where the lateral surface of this bone turns over into the dorsal surface. In many cases the sutura with the frontale coincides with this spina, so that this spina is partly built on the praefrontale, partly on the frontale.

The ligamentum is attached to this spina.

The postorbitale has on its rostral sharp ridge at a short distance dorsal to its centre a small extension, directed rostralwards.

The thin ligamentum is attached to this short extension.

8. *Ligamentum intermandibulare* (figs 11, 21 and 22; *l.i.m.*)

The ligamentum intermandibulare runs from one lower jaw to the other one. It is attached on both sides to the most rostro-medial point of the jaw. It is a thin, strong ligamentum and it has in the median a plate-formed extension, thus forming a strong connection with the glandulae submaxillares et lingualis.

D. THE MEMBRANES

Many elements consisting of connective tissue can be distinguished. They don't belong to the elements described so far and show a great difference in appearance, *e.g.* septa, articular capsules, fontanella-membranes, *etc.* Some of them will be described now in this chapter. Others will be described in the chapters devoted to the parts where they belong to.

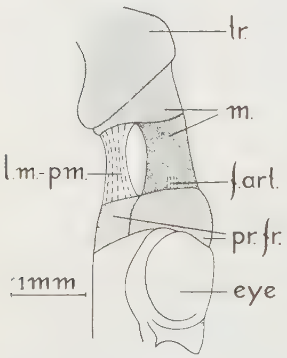


Fig. 28. Ventral view of the left orbital region. The transversum and the maxillare are moved rostro-dorsalward to show the ligamentum maxillo-praefrontale mediale. *f.art.*, connective tissue fibres in the joint between maxillare and praefrontale; *l.m.-p.m.*, ligamentum maxillo-praefrontale mediale; *m.*, maxillare; *pr.fr.*, praefrontale; *tr.*, transversum.

1. *Membrana orbitalis* (fig. 27; *mb.o.*)

This membrane occupies the area between the ligamentum orbitale superius and the frontale. It is attached to the latero-dorsal ridge of the frontale and forms the lateral part of the dorsal wall of the orbita.

Rostro-ventral to the ligamentum orbitale superius the membrane continues along the caudal side of the ligamentum maxillo-praefrontale laterale. Ventrally the membrane reaches the ligamentum orbitale. The membrane forms together with the ligaments just mentioned the dorsolateral wall of the orbita.

2. *Septum interorbitale* (figs 2 and 27; *s.i.*)

This septum forms the medial and the ventral wall of the orbita. It is attached to the crista directed laterally *(cr.p.sph.)* on the parasphenoid and the one directed medio-ventrally on the caudal surface of the praefrontale. Laterally it reaches the base of the poison-fang and the rim of the mouth.

Ventrally it joins the connective tissue of the roof of the mouth, with which it has a loose connection.

It must be remarked that the septum is paired. A small gutter is left between the septa of both sides.

E. THE ARTICULATIONS

The great movability of the different parts of the viper's skull justifies a separate description of the joints.

1. *Articulation between the cerebral skull and the supratemporale* (figs 1 and 3)

The roof of the cerebral skull has latero-caudally a triangular shallow groove *(gr.)*, bordered by the bony capsules of the canales semicirculares *(can. sem.)*. In the groove run some small bloodvessels, which are covered by a cartilaginous tissue containing many fibrils. The same tissue is found around the rostral half of the supratemporale *(s.t.)*.

The elements covered with cartilage form the articular surfaces. Dorsalwards the cartilaginous tissues of both elements change into the periost of the cerebral skull. Ventrally there exists also a connection with the periost, but this connection is weaker.

The ligamentum parieto-supratemporale *(l.p.-s.)* arises also from this cartilaginous tissue.

2. *Articulation between the supratemporale and the quadratum* (figs 7, 8 and 9)

The articular surface on the supratemporale lies on the dorsal surface of the ventro-caudal part. It occupies the area between the processus *(pr.s.t.)* and the caudal end. The surface is more or less concave and covered with the same kind of cartilaginous tissue as that of the rostral part.

The quadratum bears on its flat upper part dorsal to the small crista *(cr.q.d.)* a thick layer of cartilage. This layer is thicker on the medial than on the lateral surface of the quadratum. Moreover the medial cartilaginous layer reaches more ventralwards than the lateral one. The flat medial surface forms the articular surface.

The breadth of the flat upper part of the quadratum is about half the breadth of the articular surface on the supratemporale, and the socket around this articulation is loose, so that there can be a large space between the articular surfaces. This socket is a continuation of the outer fibrillous layer of cartilage.

3. *Articulation between the quadratum and the lower jaw* (figs 7, 8, 10 and 11)

The quadratum bears on its ventral end two knobs, a lateral one *(l.kn.)* and a medial one *(m.kn.)*, which leave a saddle-like excavation between each other.

The lateral knob is hemispherical in a lateral view. Its surface passes gradually into the surface of the body of the quadratum.

The medial knob is shorter than the lateral one and is somewhat flattened in a medio-lateral direction. The knobs, the saddle-like excavation and a part of the quadratum itself are covered by an even layer of cartilage.

The articular surface is formed by the saddle-like excavation.

The lower jaw bears also two similar knobs, resembling those on the quadratum: a rostral knob *(r.kn.)* and a caudal one *(c.kn.)*. They are placed rostrally and caudally and are partly inserted in the lower jaw. The knobs have sharper tops than those on the quadratum, and show also a saddle-like excavation between them. This saddle-like excavation is covered with a layer of cartilage which forms the articular surface. Both saddle-like surfaces are placed cross-wise on each other.

The socket around the articulation, which is a continuation of the fibrillous layer of the cartilage of both elements, is rather firm.

4. *Articulation between the quadratum and the pterygoid* (figs 5, 6, 7, 8 and 17)

The medial face of the medial knob *(m.kn.)* on the quadratum is flat and covered with an even layer of cartilage.

The pterygoid bears on its most caudal point a small spherical knob, of which the lateral face is flat and covered with an even layer of cartilage.

Both flat faces form the articulation. The socket is very thin and loose.

There exists in osteological sense no firm connection between the quadratum and the pterygoid (THILO, 1900). However, an utter independence as VERSLUYS (1936) states, does not exist either. The argument for a loose connection, that the maxillaria of both sides can be moved alternatively (PHISALIX, 1922), does not hold good.

5. *Articulation between the pterygoid and the transversum* (figs 5 and 6)

The pterygoid can be divided into a rostral narrow part and a caudal broad part (description see above). On the place where the rostral part fades into the caudal one, the pterygoid shows on its dorsal surface a slight excavation. This excavation forms the articular surface.

The transversum has caudally a spatula-shaped broadening: flat on its ventral surface, somewhat convex on the dorsal one. The ventral surface forms the articular face.

Both surfaces are connected by a firm connective tissue layer of the same thickness as each of the bones. Between the surfaces the fibres of this connective tissue layer stand perpendicularly to them. Along the borders of the faces they surround them and continue in the periost.

6. *Articulation between the transversum and the maxillare* (figs 5 and 6)

The rostral part of the transversum is broad in a latero-medial direction and flattened in a dorso-ventral direction. The rostral border is a latero-medially directed straight line. This rostral border bears an oblong knob-shaped thickening, covered with a thin layer of cartilage and forming the articular plane on the transversum.

The maxillare has about 1 mm dorsal to the basis of the poison-fang on its caudal surface an oblong round groove. This groove is dorsally and ventrally bordered by cristae. The surface of the groove is covered with a thin layer of cartilage. It forms the articular plane.

The socket around the articulation is very firm. Running from the transversum it may be considered a continuation of the periost. On the maxillare it is attached to the cristae and there it continues also in the periost.

7. *Articulation between the maxillare and the praefrontale* (figs 2 and 28)

The slightly broadened dorsal end of the maxillare has on its caudal surface a more or less triangular area, which forms the articular surface. The area is somewhat concave.

The praefrontale has a quadrangular area on the surface facing rostro-ventrally. This area is rather broad in a latero-medial direction and narrow in a rostro-caudal direction. The articular surface lies on the very lateral part of this quadrangular area. It occupies about half its surface and is somewhat convex.

Both articular faces are connected by a strong cartilaginous tissue with many fibrils (fig. 28). These fibrils run almost perpendicularly to these faces.

The articulation is surrounded by connective tissue, which continues in the periost of both parts. The articulation is rather firm, but looser than that between the pterygoid and the transversum.

F. THE GLANDS

The glands have been subjects of description of many authors (FONTANA, 1781; REICHEL, 1883; PHISALIX, 1922; WOLTER, 1924, a.o.). For detailed histological data may be referred to them. Some general facts may be mentioned for this investigation.

1. *Glandula venenata* (figs 14, 25 and 46; *gl.ven.*)

This gland lies close under the skin, in the area between the orbita and the quadratum. The glandula venenata is in a lateral view an almost triangular gland with rounded angles. In cross section it is nearly circular, being somewhat flattened in a latero-medial direction. The caudo-ventral corner shows a caudalwards directed lobe.

The general shape is rather variable, which may be due to the preservation method.

Rostro ventrally the gland turns over into the ductus venenatus *(d.ven.)*, which runs medial to the ligamentum quadrato-maxillare *(l.q.-m.)* and just ventral to the glandula Harderiana *(gl.H.)* and the eye to the maxillare *(m.)* The ductus runs just dorsal to the transversum and passes the maxillare (fig. 26) laterally over the triangular processus *(pr.m.l.)* into a rostro-ventral direction. It ends in the dorsal opening of the canal of the poison-fang *(p.f.)*. Just caudal to the maxillare, between the eye and the transversum, the ductus has a thickening, formed by a small gland, the glandula venenata accessoria *(gl.ven.acc.)* (WOLTER, 1924; RADOWANOVIC, 1928).

The glandula venenata and the ductus venenatus are surrounded by a connective tissue bag, to which are attached the musculus adductor externus superficialis 2 *(m.a.m.e.s.2)*, the musculus adductor externus profundus *(m.a.m.e.p.)*, the ligamentum quadrato-maxillare *(l.q.-m.)* and the ligamentum supratemporale-glandulare *(l.s.-gl.)*.

The interior of the gland (fig. 46) is divided into three or four parts by connective tissue plates, which lie in a latero-medial plane. Against these connective tissue plates smaller plates are found, surrounding holes and tubes. Along the walls of these holes and tubes lie the small glandular cells (see also fig. 163 in FAHRENHOLZ, 1937).

The glandula venenata accessoria consists of small tubes, which empty themselves into the ductus venenatus.

2. *Glandula Harderiana* (fig. 25; *gl.H.*)

This gland lies caudal and ventral to the eye.

The main part is situated caudal to the orbita. The somewhat lobed gland is more or less quadrangular in a lateral view. In cross section it is circular.

Rostro-ventralwards it narrows and occupies the caudo-ventral corner of the orbita. The form of this part is sickle-shaped in transverse section. The concave side of this rostro-ventral part joins the eye, the convex side joins the roof of the mouth and the pterygoid. Still rostralwards, running between the eye and its muscles, it is a tube. Rostro-ventral to the eye the tube widens and runs through a small foramen in the praefrontale. This foramen lies close and ventro-lateral to the centre of the praefrontale. The tube turns medialwards and empties itself into the mouth-cavity. This opening is next to that of the organ of Jacobson.

The inner structure consists of small lobes, of which the walls are covered with gland-cells that leave only a small lumen between them. There is no special arrangement in the lot of lobes. The tube ventral to the eye is rather narrow and surrounded by gland-cells. Just caudal to the praefrontale the diameter of the tube enlarges, whereas, when the gland runs through the foramen and rostral to it, the diameter narrows. In the part that runs from the praefrontale medialwards the gland-cells are lacking.

3. *Glandula nasalis externa* (figs 4 and 29)

This gland lies rostral to the praefrontale between the skin and the septomaxillare.

From the septomaxillare *(s.m.)* runs a connective tissue plate to the lateral edge of the nasale *(nas.)* and the medio-rostral edge of the praefrontale. This connective tissue plate is ventrally connected with the praemaxillare *(pr.m.)* and the ventral edge of the praefrontale.

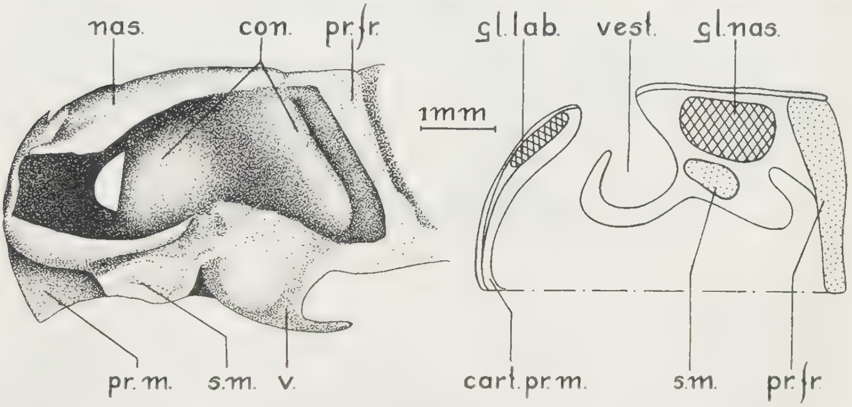


Fig. 29. Sections through the olfactorial region. a, paramedial section seen from medial; b, diagram of a frontal section halfway dorsal and ventral surface. *cart.pr.m.*, cartilaginous part on the praemaxillare; *con.*, conchae; *gl.lab.*, glandula labialis; *gl.nas.*, glandula nasalis; *nas.*, nasale; *pr.fr.*, praefrontale; *pr.m.*, praemaxillare; *s.m.*, septomaxillare; *v.*, vomer; *vest.*, vestibulum.

From the lateral edge of the praefrontale runs a second connective tissue plate rostralwards to the praemaxillare, just under the skin. This plate is connected with an other connective tissue plate, on the same level with the rostral edge of the septomaxillare, by a part of this septomaxillare which runs lateralwards.

The space between these connective tissue plates is filled up by the gland. The general shape of the gland is about spherical, though rather irregular.

The tube opens into the caudal wall of the vestibulum nasale, near the nostril.

The interior consists of rather small lobes. The walls of the lobes are covered with gland cells of about the same size as those of the glandula Harderiana. The tubes left between the cells have a larger diameter than those of the Harderian gland.

4. *Glandula labialis superior* (fig. 29; *gl.lab.*)

This gland lies along the dorsal margin of the mouth. It runs caudalwards from the most rostral point of the head to a point at a short distance from the corner of the mouth. The gland lies lateral to the adductor muscles, just under the skin. Over the greater part of the distance the skin forms a distinct lip-like hem, circular in transverse section. The caudal part of the gland is rather narrow, lateral to the praemaxillare it is broadened. Rostral to the glandula nasalis externa the gland continues as the glandula rostralis and becomes much bigger. It is extended from the dorso-rostral part of the skin to the ventral part. Rostrally the glands of both sides join each other.

The inner structure is of the same character as that of the glandula nasalis, the cells are a little smaller.

The excretory ducts are numerous, especially in the rostral part. The ducts are small tubes, which run ventro-medialwards and open into the mouth-cavity.

5. *Glandula labialis inferior*

This gland lies along the ventral margin of the mouth. This gland nearly equals the glandula labialis superior. It is quite as long as this one and it lies in an equal position in the lower lip. It is of about the same shape in transverse section, only it broadens more caudally, *i.e.* lateral to the caudal tooth on the dentale. A big rostral part does not exist. The inner structure equals that of the glandula labialis superior.

6. *Glandula submaxillaris* (fig. 21; *gl. subm.*)

This gland lies paramedially, just caudo-ventral to the ligamentum intermandibulare. It is a small bottle-like gland with a smooth surface.

The excretory duct is attached to the caudal extension of the ligamentum intermandibulare and opens into the mouth-cavity.

The inner structure of the gland equals that of the glandula Harderiana.

The gland is covered ventrally by the musculus intermandibularis anterior part 4, which is attached to it.

7. *Glandula sublingualis* (fig. 21; *gl.subl.*)

This gland lies ventral to the connective tissue bag around the tongue.

It is an oblong unpaired gland of an irregular shape. The gland is twice as long as the glandula submaxillaris; it reaches from a short distance from the tongue-bone in retracted position to a point just caudal to the ligamentum intermandibulare.

The excretory duct opens caudal to the outlet of the glandula submaxillaris into the mouth-cavity. The inner structure is the same as that of the glandula submaxillaris.

G. THE BRAIN (figs 30, 31 and 32)

For a description of the general outer shape of the brain of snakes may be referred to the handbooks (HOFFMAN, 1890; HALLER VON HALLERSTEIN, 1934).

The telencephalon of the viper runs in the skull from the ethmoidal region to the canales semicirculares. In the median the caudal border is situated more rostrally.

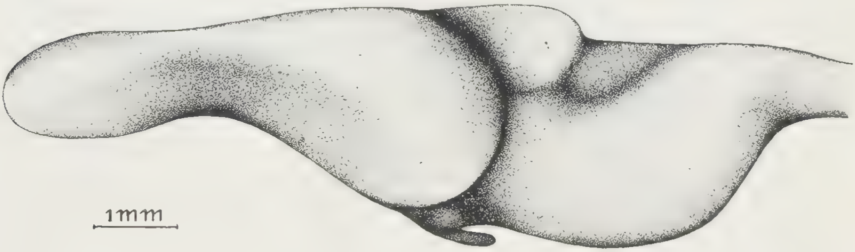


Fig. 30. Lateral view of the brain.

Between the orbitae the telencephalon is relatively long, nearly as broad as high. Just behind the orbitae it is spherically extended in a lateral and a ventral direction. The roof is slightly domed. In the median, between the parts of both sides, is left a shallow groove.

The lateral side of the telencephalon is facing ventro-laterally, rostrally this side is spherical (lobus olfactorius), between the orbitae it is concave, and in the caudal part it is spherical again. The transition of the dorsal into the lateral surface is rounded. In a lateral view the border-line between these surfaces is curved in that way that the rostral and the caudal parts of this line are more ventral than its centre part.

The bottom shows in a lateral view a waved line, of which the rostral and the caudal part are situated ventrally in regard to the centre part between the orbitae.

The entire surface of the telencephalon is smooth. The length in the median is about 6 mm. The greatest breadth is about 6 mm; the narrowest part is about 2 mm. The height varies from 1.5 mm to 3 mm.

The mesencephalon lies caudal to the telencephalon. It is a spherical part with a diameter of about 1.5 mm. Rostrally and ventrally it is continuously connected with the other parts of the brain.

The diencephalon lies ventral to the mesencephalon and ventro-caudal to the telencephalon. It has a spherical shape. A sharp demarcation between mesencephalon and diencephalon does not exist.

The metencephalon is a flat disc, extended from the mesencephalon caudalwards and covering the tela chorioidea.

The myelencephalon reaches from the most caudal point of the telencephalon to the foramen magnum. The surface is spherical, except the roof of the fourth ventriculus. This roof is a folded layer under the cerebellum. The remaining part of the roof of the myelencephalon lies at the same level. The lateral surface is extended lateralwards from the foramen magnum.

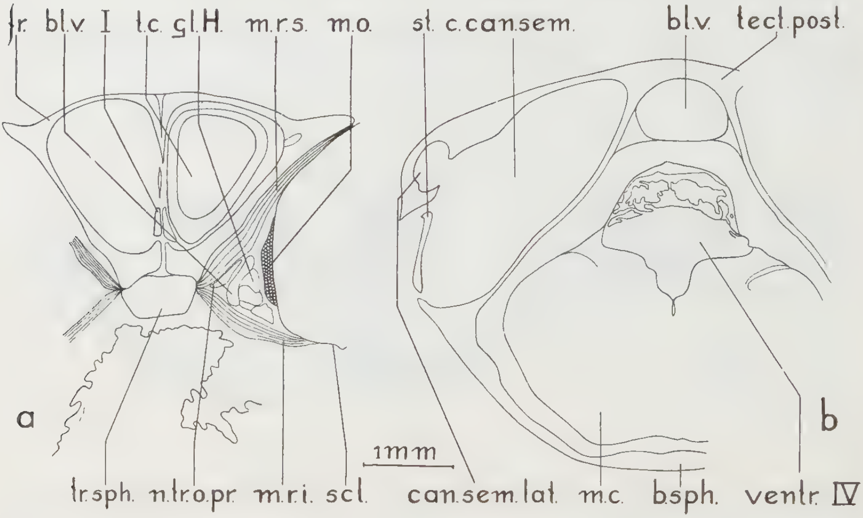


Fig. 31. Transverse sections through the brain and surrounding elements. a, section in the orbital region; b, section in the otical region. *bl.v.*, bloodvessel; *b.sph.*, basisphenoid; *c.can.sem.*, cavity of the canales semicirculares; *can.sem.lat.*, canalis semicircularis lateralis; *fr.*, frontale; *gl.H.*, glandula Harderiana; *m.c.*, myelencephalon; *m.o.*, musculus obliquus; *m.r.i.*, musculus rectus inferior; *m.r.s.*, musculus rectus superior; *n.tr.o.pr.*, nervus trigeminus ophthalmicus profundus; *scl.*, sclera; *st.*, stapes; *t.c.*, telencephalon; *tect.post.*, tectum posterius; *tr.sph.*, trabecula sphenoidea; *ventr. IV*, fourth cerebral ventriculus; *I*, nervus olfactorius.

The ventral surface is a curved plane, extended far ventralwards from the foramen magnum. Caudo-ventral to the lobi optici between the surfaces of the myelencephalon and the cerebellum runs a groove from rostro-ventral to dorso-caudal.

The origin of the nerves does not lead to any special description. We may refer to the handbooks.

H. THE NERVES (figs 1, 32, 33, 34 and 35)

A description of the course of the nerves will be given so far as useful for a more detailed investigation on the construction of the head. We only mention those nerves that are of importance.

The course of the nervus olfactorius, the nervus opticus, the nervus oculomotorius, the nervus trochlearis, and the nervus abducens does not lead to any special description.

The nervus trigeminus, divided into three rami, leaves the cerebral skull through three foramina *(for.opt., for.*V^2*, for.*V^3*)*. The nerve starts from the brain as a branch which runs through a large foramen *(for. trig.)*. This foramen is covered laterally by a bony plate of the outer surface of the cerebral skull. The opening in the outer wall is formed by two foramina, a rostral *(for.*V^2) and a caudal one *(for.*V^3*)*. From the

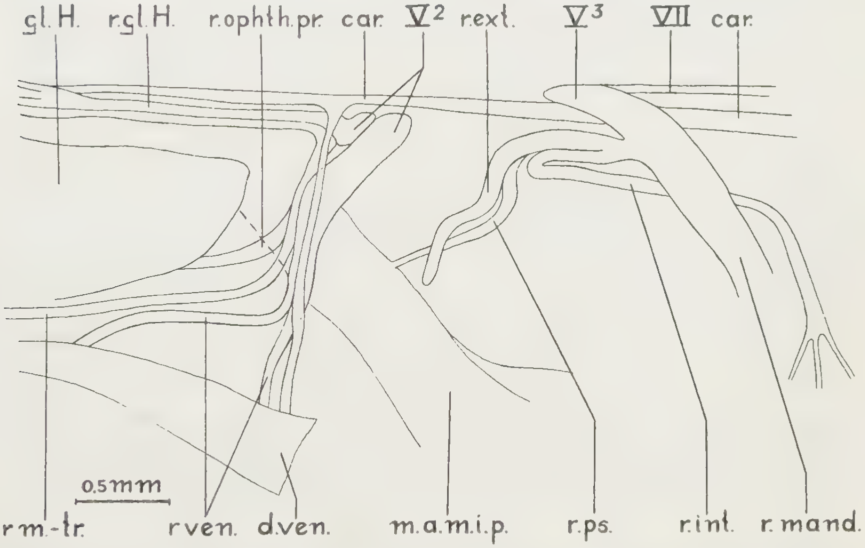


Fig. 32. Lateral view of the left nervus trigeminus. *car.*, arteria carotis; *d.ven.*, ductus venenatus; *gl.H.*, glandula Harderiana; *m.a.m.i.p.*, musculus adductor mandibulae internus pseudotemporalis; *r. ext.*, ramus to the musculus adductor mandibulae externus; *r.gl.H.*, ramus to the glandula Harderiana; *r.int.*, ramus to the musculus adductor mandibulae internus pterygoideus; *r.m.-tr.*, ramus to the maxillare and the transversum and surrounding parts; *r.mand.*, ramus mandibularis; *r.ophth.pr.*, ramus ophthalmicus profundus; *r.ps.*, ramus to the musculus adductor mandibulae internus pseudotemporalis; *r.ven.*, ramus venenatus; V^2, nervus trigeminus ramus maxillaris; V^3, nervus trigeminus ramus mandibularis; *VII*, nervus facialis.

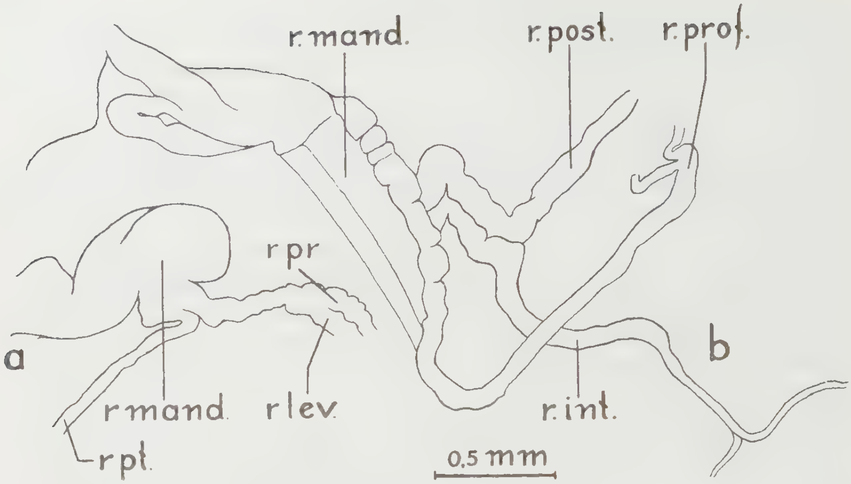


Fig. 33. Lateral view of the caudal branches of the left nervus trigeminus. a, medial branches. b, lateral branches. *r.int.*, ramus to the musculus adductor mandibulae internus pterygoideus; *r.lev.*, ramus to the musculus levator pterygoidei; *r.mand.*, ramus mandibularis; *r.post.*, ramus to the musculus adductor mandibulae posterior; *r.pr.*, ramus to the musculus protractor pterygoidei; *r.prof.*, ramus to the musculus adductor mandibulae externus profundus; *r.pt.*, ramus to the pterygoid and its surrounding parts.

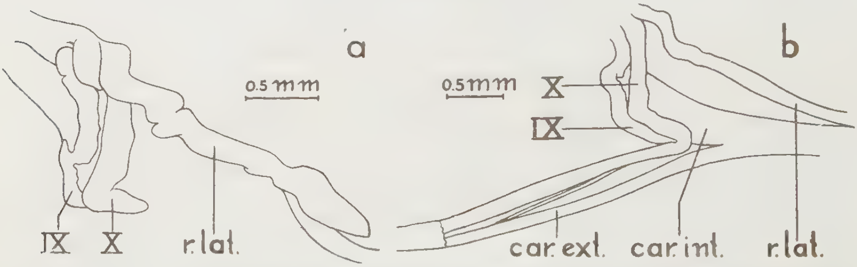


Fig. 34. The course of the nervus glossopharyngeus and nervus vagus behind the quadratum-lower jaw joint. a, lateral view; b, ventro-lateral view. *car.ext.*, arteria carotis externa; *car.int.*, arteria carotis interna; *r.lat.*, ramus lateralis nervi vagi; *IX*, nervus glossopharyngeus; *X*, nervus vagus.

cavity between the internal large foramen and the lateral cover, starts rostrally a small foramen *(for. V^1)*, which debouches into the cerebral capsule.

The first ramus (V^1) of the nervus trigeminus leaves the cerebral skull through this internal large foramen *(for.trig.)*. It reenters the cerebral skull through the small foramen *(for.V^1)* and runs rostralwards lateral to and between the telencephalon and the diencephalon. It runs on along the ventral side of the telencephalon and leaves the cerebral capsule again through the foramen opticum *(for.opt.)*. It innervates the glands of the head and the connective tissue in the ethmoidal region.

The second ramus (V^2) leaves the cerebral skull through the rostral large foramen (*for.*V^2). It is divided into two branches, a thick caudal one and a thinner rostral one. In many cases the rostral branch lies more or less ventrally. The thick caudal branch runs ventralwards lateral to the musculus pseudotemporalis *(m.a.m.i.p.)* to the ductus venenatus *(d.ven.)*. Lateral to the musculus pseudotemporalis it branches off the ramus ophthalmicus profundus *(r.opht.prof.)*. Just before reaching the ductus venenatus the caudal branch splits into two parts *(r.ven.)*. Both parts lie in a S-shaped curve.

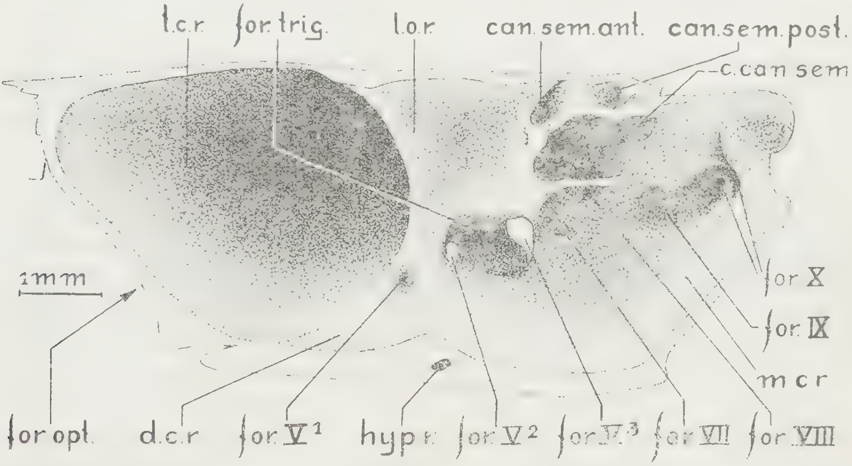


Fig. 35. Medial view of a paramedial section of the cerebral skull. *c.can.sem.*, cavity for the static organ; *can.sem.ant.*, canalis semicircularis anterior; *can.sem.post.*, canalis semicircularis posterior; *d.c.r.*, diencephalon room; *for.opt.*, foramen opticum; *for.trig.* foramen nervi trigemini; *for.*V^1, foramen for the nervus trigeminus, ramus ophthalmicus superficialis; *for.* V^2, foramen for the nervus trigeminus, ramus maxillaris; *for.* V^3, foramen for the nervus trigeminus, ramus mandibularis; *for. IX*, foramen for the nervus glossopharyngeus; *for. X*, foramen for the nervus vagus; *hyp.r.*, part of the room occupied by the hypophyse; *l.o.r.*, lobi optici room; *m.c.r.*, myelencephalon room; *t.c.r.*, telencephalon room.

The thin rostral branch is divided into two parts: one part *(r.gl.H.)* runs straight rostralwards, dorsal to the glandula Harderiana. The other part *(r.max.-tr.)* runs ventralwards and bends rostralwards between the glandula Harderiana and the transversum.

The third ramus of the nervus trigeminus leaves the cerebral skull through the caudal large foramen (*for.* V^3). At a short distance from this foramen it splits into three small branches, of which two run rostralwards and one medialwards, and a main branch. One rostral branch is divided into two parts *(r.ps., r.ext.)*, which innervate the musculus adductor mandibulae internus pseudotemporalis and the musculus adductor mandibulae externus. The second rostral branch *(r.int., r.post.)* turns after a short rostral course caudalwards and innervates the musculus adductor mandibulae internus pterygoideus and the musculus adductor posterior.

The third branch *(r.pr., r.lev.)* runs rostro-medialwards and innervates the musculi levator et protractor pterygoidei and protractor quadrati.

The main branch *(r.mand.)* of the third ramus of the nervus trigeminus runs caudalwards, bends ventralwards and enters the lower jaw.

All branches of the third ramus of the nervus trigeminus show many short twistings in their courses.

The nervus facialis has in a lateral view partly the same outlets as the nervus trigeminus. The branches that run together with the nervus trigeminus cannot macroscopically be distinguished from it. Special attention may be paid to the third branch. This branch runs through the foramen VII *(for. VII)* along the columella auris to the ventral part of the musculus depressor mandibulae. This branch has no twistings.

The nervi glossopharyngeus *(IX)* et vagus *(X)* are hardly to be separated. For a general description of their outlets in the cerebral skull and their courses may be referred to HALLER VON HALLERSTEIN (1934) and to fig. 35.

Important in our study is the fact that these nerves run caudalwards, partly to the body *(e.g.* ramus lateralis nervi vagi *(r.lat.))*, partly to the musculi intermandibulares and the tongue-muscles and -bone. When passing the joint between the quadratum and the lower jaw the branches of the nerves show many short spiral twistings (fig. 34). Two thick branches run on rostralwards to the tongue-muscles.

I. THE BLOODVESSELS (figs 32 and 34)

For a description of the course of the bloodvessels may be referred to PHISALIX (1922). Special attention may be paid to the course of the arteria carotis (*car.*) indicated in figures 32 and 34.

J. THE EYE AND SURROUNDING PARTS (figs 1, 2, 27 and 31)

The eye of the viper shows no special macro-morphological differences from other snake-eyes. For a description of the shape of these eyes may be referred to FRANZ (1934).

The orbita is almost four times bigger in volume than the eye itself. It is built partly of bone, partly of membranes (see above). The orbita is filled by the glandula Harderiana (see the description of this gland), muscles, nerves and bloodvessels (fig. 31).

K. THE ETHMOIDAL REGION (figs 4, 27 and 29)

The general shape of the capsula nasalis is spherical, a little flattened in the median where the spheres of both sides meet each other.

The nostril lies in the lateral surface of the sphere. From the nostril the nasal tunnel runs medialwards and a little rostrally, then turns paramedially straight caudalwards. Caudally, close to the bent, the tunnel shows in a lateral direction a broadening, behind which it narrows again and then continues lateralwards over a short distance. The tunnel is not spherical, but flattened medially. It shows ventrally an almost flat floor through the presence of some strong other elements.

The lateral wall bears two conchae (fig. 29). The rostral one is a curved, standing, cartilaginous plate, forming in its lateral concave side the vestibulum. The dorsal and the ventral part of this plate are a little curved laterally. The second, caudal concha is longer and narrower and partly supported internally by a flat and narrow processus *(c.l.w.)* of the septomaxillare, directed dorsally.

The medial wall of the tunnel is rostrally formed by the praemaxillare and the septomaxillare and caudally by the vomer, which lie in a line just in the median plane.

The rostral wall is mainly formed by strong connective tissue membranes, supported by cartilage. Only the rostro-medio-ventral corner is occupied by the praemaxillare.

The dorsal wall of the tunnel is also formed by strong connective tissue with cartilage. However, the most dorsal and the centre part are formed by the bony triangular hood of the nasale.

Caudally the nasal region is bordered by the praefrontale, which has a concave rostral face.

The ventral wall of the tunnel is quite complex. Rostrally lies paramedially the praemaxillare, caudally and laterally is the same connective tissue plate with cartilage as mentioned above.

The caudal part of the ventral wall is formed by the septomaxillare. The septomaxillare *(s.m.)* is a flat long bone, ending on both sides in processus lying medially and laterally. The lateral one bears a processus *(c.l.w.)* directed dorsally. Firmly connected in the median with the medial processus of the septomaxillare lies the vomer. The vomer is a bladder-like bone with three processus: a rostrally directed one, a medio-caudal directed one and a latero-caudal directed one. Between the caudally directed processus is situated the choane. Rostrally, close to the choane, opens into it the organ of Jacobson, which lies in the vomer.

For a detailed description we may refer to BROMAN (1918) and KAHMANN (1932).

L. THE STATO-ACOUSTIC ORGAN

This organ was described by RETZIUS (1884) in *Vipera rhinoceros* and *Vipera berus*. We may refer to that description.

The lateral semi-circular canal lies laterally almost parallel to the median. The anterior semi-circular canal runs from caudo-medial to rostro-lateral, the posterior one from rostro-medial to caudo-lateral. The commissura lies medial to the horizontal canal. The bony capsule surrounding this commissura lies in the groove between myelencephalon and cerebellum, mentioned above.

The columella auris (figs 1, 8 and 31) runs from the quadratum to the fenestra ovalis *(fen.ov.)*. The articulation with the quadratum is formed by the end of the cartilaginous extracolumella and the most dorsal part of the crista quadrati *(cr.q.)*. The columella consists of two parts of equal length: the cartilaginous extracolumella, lying laterally, and the bony stapes, lying medially. The stapes ends medially in an ellipsoid plate, which is connected with the ridge of the fenestra ovalis by a membrane.

M. THE FEEDING MECHANISM (fig. 36)

Before swallowing the prey the viper kills it by means of a poison injection. The movements for the injection act equal those of many Solenoglypha (HAAS, 1930; KLAUBER, 1939 a.m.o.). The injection occurs by a poison-fang *(p.f.)*, which is stung with strong power into the prey. The fang has a canal through which the poison, excreted by the poison-gland, flushes into the wound. Before the fang can be stung the mouth must be opened and the maxillare *(m.)*, in which the fang stands, erected. The beat of the head towards the animal, the opening of the mouth and the injection of the poison occurs in about 1/40 sec. This is too quick to observe the movement but for the help of a slow-motion film. With the aid of such a film it was possible to see that the head is lifted rostrally and that the movements of the upper jaw (erection of the maxillare) and lower jaw occur simultaneously. Probably both movements are coordinated. During the injection act, as far as could be observed, the lower jaw is lifted, just the opposite of what was observed by VAN RIPER (1953) in *Crotalus* sp. The injection act could hardly be watched. Probably the movement of the bony parts does not differ essentially from that in the swallowing act. After the injection the viper draws its head back and leaves the prey till it is killed by the poison. Sometimes the poison-fang cannot be drawn back momentaneously and then it often results in a basal break of the fang. The dying of the prey takes about fifteen minutes.

A short time after the death of the prey the snake starts looking for it, using its tongue in combination with the organ of Jacobson and the nose as smell receptors (BAUMANN, 1929) to find the prey. The snake smells at the prey until it has found the head and begins to swallow it.

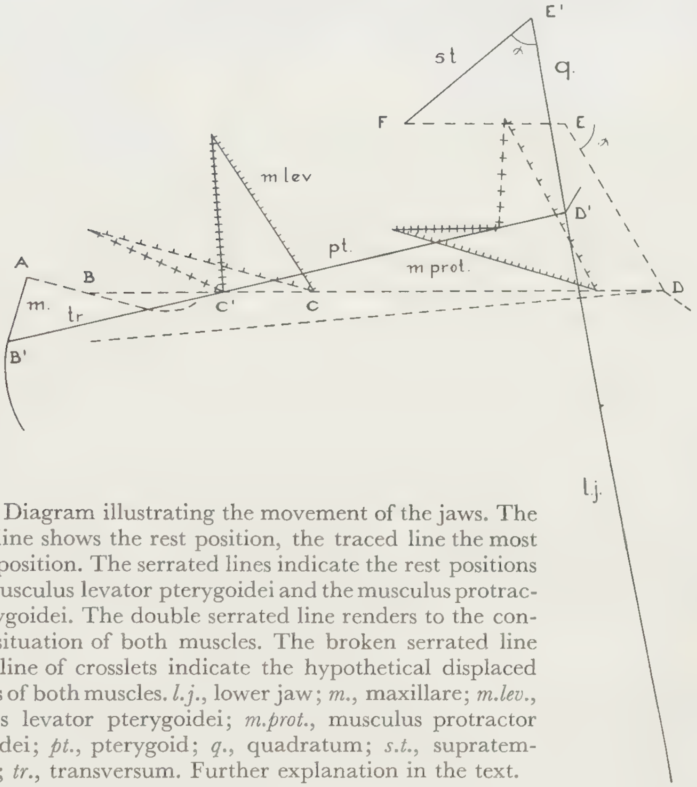


Fig. 36. Diagram illustrating the movement of the jaws. The broken line shows the rest position, the traced line the most opened position. The serrated lines indicate the rest positions of the musculus levator pterygoidei and the musculus protractor pterygoidei. The double serrated line renders to the contracted situation of both muscles. The broken serrated line and the line of crosslets indicate the hypothetical displaced positions of both muscles. *l.j.*, lower jaw; *m.*, maxillare; *m.lev.*, musculus levator pterygoidei; *m.prot.*, musculus protractor pterygoidei; *pt.*, pterygoid; *q.*, quadratum; *s.t.*, supratemporale; *tr.*, transversum. Further explanation in the text.

The first movement is a normal bite. The prey is fixed between the upper jaws and the lower jaws. Then the upper and lower jaw at one side release and the upper jaw of that side is moved forward. At the same time the articulation between the quadratum *(q.)* and the lower jaw *(l.j.)* of that side is moved forward. The lower jaw elevates and the prey is fixed between the jaws. After the fixation at this side the jaws at the other side relax, move forward and close, *etc.*

The forward movement of the old upper jaw is connected with an elevation of the caudal part of the upper jaw. The quadratum moves also dorsalwards thus pushing the caudal point of the supratemporale *(s.t.)* medio-dorsalwards. Observations of an eating snake by film and by naked eye also show this way of moving.

It is obvious that the description given by many authors (Gadow, 1901; Phisalix, 1922; Haas, 1931 a.o.) of a movement of the supratemporale directed ventralwards from the rest position is a mistake, since a ventralward movement of the upper jaw would not enlarge the mouth-cavity, but just the opposite. Some circumstances proving the impossibility of a ventralward movement of the supratemporale when the maxillare is erected are first the position of the protracting muscles, which can only elevate the upper jaw, and secondly the occurrence of a ligamentum parieto-supratemporale (fig. 3; *l.p.-s.*).

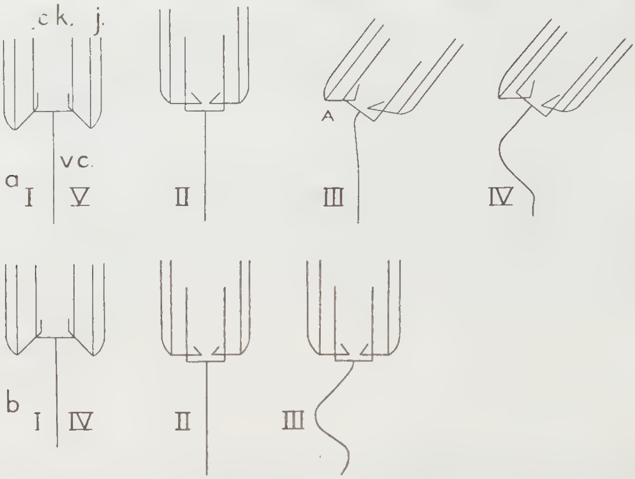


Fig. 37. Diagram showing the different stages of the movement of the cerebral skull to the jaws in the swallowing act caused by the activity of the cervical muscles. a, the movement in the viper; b, the movement in the python. *c.k.*, cerebral skull; *j.*, jaw; *v.c.*, vertebral column.

In many cases the maxillare is only more or less erected, though several authors suppose the maxillare is not erected during the swallowing act. Certainly, the maxillare turns over a smaller angle during the swallowing act than during the act of the poison injection. The occurrence of an articulation between transversum and pterygoid makes a more or less retracted position of the maxillare possible (see later on). Besides, a turn of the upper jaw around the longitudinal axis of its rostral parts may favour this situation. When the old upper jaw turns around this axis the quadratum is moved dorsalwards and a little medialwards, so that the supratemporale moves also medialwards, without an erection of the maxillare. The movement of the articulations between quadratum and lower jaw, and between quadratum and supratemporale can be observed indirectly by slow-motion pictures.

When both pairs of jaws are placed in the most forward position, the prey has been taken in over a short distance, and now the cerebral skull must be pushed forward. The same movements are repeated then. Sometimes the prey is very big. In that case the muscles serving for the forward movement of the cerebral skull work simultaneously with the cervical muscles. The neck is successively bent and stretched, so that the cerebral skull is pushed forward (fig. 37). Often a combination can be observed of the movements of the jaws with a bending in the neck region. This bending means for every forward movement of the upper jaw a greater forward movement over the prey. Most authors (FONTANA, 1781; KATHARINER, 1900; PHISALIX, 1922; WOLTER, 1924; HAAS, 1931) agree in the observations of the movements of the jaw as far as they have studied them. No notes could be found in literature about which part the neck region plays in the food-intake. It is doubtless, however, that the moving of the neck region is necessary when swallowing preys and many snakes use it *(e.g. Python)*.

It must be remarked here, that sometimes the snake moves backward instead of pushing the skull forward. This can be explained as follows.

When the snake bends its neck region the head is lifted a little, so that the rest of the snake's body remains at the same place and only the rostral part of the cervical region is bent. When, however, this bent part is stretched to push the skull forward, the jaws holding the prey must be pressed on the ground. In that case it may happen that, if the pressing power is rather strong, or the prey is big and heavy, the body is pushed backward. An indication for the importance of the weight of the prey in this rather useless movement is the fact that the backward movement is mainly observed at the start of the swallowing.

The roles played by the different members in the feeding-mechanism will be discussed in the following chapters.

IV. THE GENERAL CONSTRUCTION OF THE VIPER'S HEAD

In the head of an animal can be distinguished functions on different levels. These functions are realized in structural elements, called functional components, constructions *etc*. The way in which the realization has taken place is in many cases difficult to prove. At one hand the rules for realization can be investigated by experimental and theoretical methods, on the other hand by a comparative method.

In the viper's head seven main functions are realized, concerning the way of living. They are called: feeding, seeing, smelling, orientation, respiration, coordination and creeping.

The realization of the feeding depends on the way of feeding and on the kind of food. The relatively enormous prey leads for many snakes to the well-known swallowing apparatus: the loosely connected upper jaw and the lower jaw. The independent situation of the jaws of both sides is constructively difficult to understand. The movement of the jaws independent of each other has some significance in the swallowing act, although in snakes with less movability of the jaws the swallowing occurs mainly by a distinct activity of the cervical muscles.

It seems more plausible to consider the loose connection as a consequence of the special kinetic situation (Versluys, 1902, 1936), *i.e.* a firmly closed cerebral skull and a relatively small olfactorial capsule. The peculiar way of killing the prey (a necessity for eating an enormous prey) is realized for the viper in the poisoning apparatus. The detailed structure of both apparatus depends on the requirements of the function, on the influence of the members of the apparatus on each other, and on the influence of other functional components (see following chapter).

The realization of seeing is the eye, which must have a spherical shape (Trendelenburg, 1943). The volume of the eye is to depend on the size of the animal and the required sight (Franz, 1934; *cf.* for literature Van der Klaauw, 1943).

The realization of smelling is the nose and the organ of Jacobson. The functional relation between both organs is close, but the relation between form and function is unknown, and so is the share in the function of each of the organs (Broman, 1919; Kahmann, 1932).

The realization of the orientation is found in the canales semicirculares. On this structure no data are found concerning the relation between form and function although many facts are known of the function.

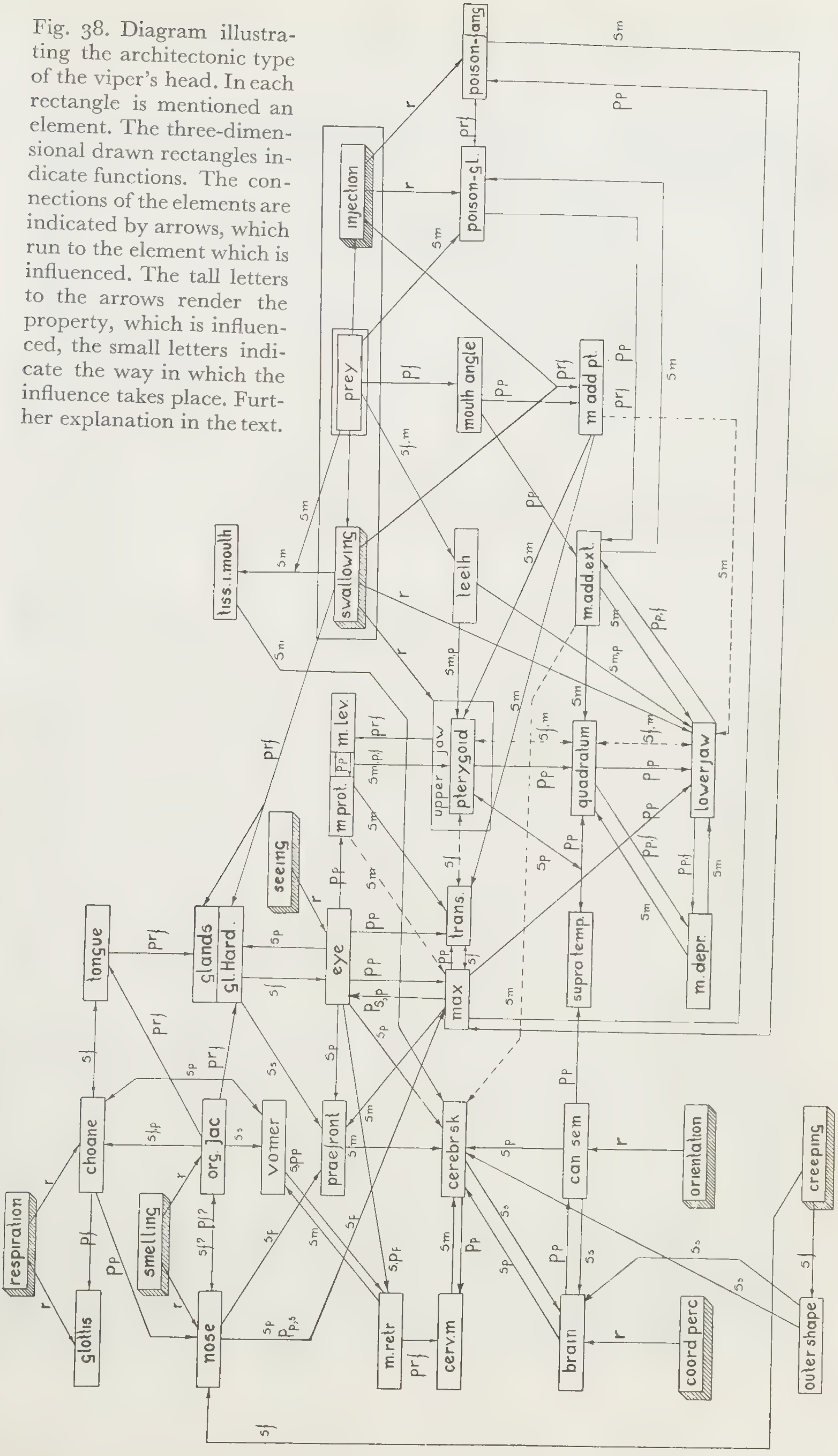
In the head some small organs, the glottis and the choane, are realizations of a part of the respiration function.

The function of coordination is realized in the brain. A relatively big size of the brain in a small animal was already known to Cuvier, Marsh, and Dubois (for literature see Van der Klaauw, 1948). Besides some parts, *e.g.* the telencephalon and the myelencephalon, are well developed. This development is in agreement with the great area of innervation of their nerves. The brain must therefore for the greater part be considered dependent on the other functions.

The function of creeping has no directly structural realization in the head, but the outer shape of the head must be in accordance with the peculiar way of moving.

Up to recently the relations between form and function were of less interest in research. Most studies have been made to detect the function

Fig. 38. Diagram illustrating the architectonic type of the viper's head. In each rectangle is mentioned an element. The three-dimensional drawn rectangles indicate functions. The connections of the elements are indicated by arrows, which run to the element which is influenced. The tall letters to the arrows render the property, which is influenced, the small letters indicate the way in which the influence takes place. Further explanation in the text.



of a special element or to know the structure by which a certain function is managed. A general connection between both fields of research has been lacking.

Starting from the given realizations as structural facts, the problem of their integrations and their mutual influences is object of this research.

In the diagram of figure 38 the influences are indicated by arrows running to the influenced elements, the rectangles. The realizations of the functions (three-dimensional rectangles) are marked with r. The big letters render the property which is influenced: P., position; S., structure; Pr., presence. The small letters added as indices to the big ones show the way of influencing: p., by the position of the influencing element; s., by the structure; m., by the mechanical influence; f., by any functional influence, though not in a mechanical way.

Some influences of less importance are not indicated and some elements should have been divided into more than one part or into smaller elements.

In the general construction of the head the eye and feeding mechanism play a dominant rôle. In this discussion will be started from the assumption that the eye has a minimum volume and that in a small animal the eye is relatively big (FRANZ, 1934). The position of the eye in lateral direction may partly be determined by the brain; a superficial view, however, on skulls of related snakes (*Lachesis*, *Crotalus*, *Bitis*) shows a far lateral position independent of the brain. In those cases the position of the eye is determined by the outer surface of the head. The outer surface of the head coincides with the lateral side of the maxillare, so that the breadth of the head depends on the breadth of the maxillare added to the room left between both maxillaria. This room is occupied by the olfactorial capsule, of which the position is understandable by its close connection with the telencephalon and the functional requirement of a relatively far rostral position of the poison-fang *mutatis mutandis* the maxillare.

The influence of the eye on the brain is to depend then on the entire breadth of the head and the extension of the eye and the brain. Consequently in smaller snakes the brain is partly invaginated by the eye and in bigger ones the outer surfaces of brain and eye have hardly any connection.

Many parts are influenced by the position of the eye. First the transversum, of which the most dorsal position is close to the eye and ventral to it, consequently the place of the articulation with the maxillare is also determined. Because the maxillare lies far rostrally there is no possibility of muscles attached to it that serve directly for its turning. The movement of this bone must be managed then by a pulling act from caudally. This pulling act may be caused by a muscular system via a caudalwards running bone. The muscles that can do so, must be situated between this bone (the upper jaw) and the neurocranium.

As will be proved in the discussion of the muscles, the position of the eye bounds rostrally the place of attachment and the position of the musculus levator pterygoidei and of the musculus protractor pterygoidei.

The contraction of the musculus levator pterygoidei and the musculus protractor pterygoidei causes a rostralward and a dorsalward movement of the upper jaw. Since, however, the distance between both articular surfaces on the maxillare has a minimum value, the articulation with the transversum must be moved ventralwards during the turn of the maxillare. The distance between the transversum and the neurocranium becomes longer. Consequently the caudal part of the old upper jaw will be moved dorsalwards. The point that *can* relatively remain in position in lateral projection is the most rostral place of attachment of the musculus levator pterygoidei on the old upper jaw. This point, however, must remain caudal to the orbita in every position of the jaw. And so the conclusion may be drawn, that the rostral part of the old upper jaw must have the length of the orbita added to the rostral displacement of the old upper jaw.

The caudal part of the old upper jaw serves for the attachment of the musculus protractor pterygoidei. The angle between the muscle fibres and the pterygoid is very small, so that the fibres of this muscle must have a length of about twice the distance of the rostral displacement of the articular point with the transversum on the maxillare. The rostral displacement of this articular point is to depend on the distance between the articulation on the maxillare and on the angle over which the maxillare is moved. The distance of the articulations on the maxillare has a minimum value, as is pointed out. The angle must be about 90°, fitting in with the curve and the length of the poison-fang as will be shown later on. The rostral displacement will be then 2.5–3 mm. The rostral part of the area of attachment lies close behind the eye, consequently the pterygoid has a determined length. The numbers for these lengths are:

displacement of the maxillare-transversum joint: 2.5–3 mm *i.e.* 0.5–1 mm rostral to the orbita; length of the orbita: 5.5–6.5 mm; length of the muscle fibres: 5–6 mm; entire length of the old upper jaw: about 14 mm, *i.e.* almost 2 mm length remaining for the area of attachment of the muscle fibres, representing the breadth of the muscle.

The construction of the mechanism effects a minimum dorsalward movement of the caudal part of the pterygoid. This movement causes a displacement of the quadratum and a medio-dorsalward one of the supratemporale.

Between the quadratum and the supratemporale exists a certain relation (fig. 36). Supposing the caudal point of the pterygoid moves from D to D^1 in the figure. The point E must shift rostralwards; a caudalward movement is impossible because of the rostral position and the inextensibility of the supratemporale. The question is now on or near which point E^1 must lie. The properties of the joint and its surrounding tissue only permit a position of the bony elements, which deviates only 30° from a perpendicular position. Consequently the angle (α) between both elements or their production must remain greater than 60°. Given the position of the rostral point of the supratemporale, F and α, it follows that only one situation can occur and that the lengths of both bony elements are determined.

This described constructive situation makes it understandable, that Haas (1931) could not find a direct correlation between the length of the quadratum and the size of the prey. A correlation between the size of the poison-fang and the length of the quadratum is quite improbable, because the quadratum does not move ventralwards, as Haas (1931) assumes, but dorsalwards.

The precise adaptation of the bony elements to each other, thus forming a total construction, should give only one possibility of movement. The exact determination of the movement, however, can be diminished more or less by the rather loose connection of the tissue around the joint. Moreover, the movement is not exactly determined in one plane.

Nevertheless a problem arises, if the point F lies so near the median that the point E^1 should have to shift over the median. The articular points, E^1, of both sides can meet in the median, however, they cannot be pushed farther. This situation occurs. If the point D must be moved to D^1 due to the construction of the other parts in the upper jaw, then the quadratum should be shortened during the dorsalward movement. This shortening of the quadratum in ventro-dorsal direction is caused by a turn lateralwards of its distal point. This turn is possible by a bend in the pterygoid and by a rather loose connection with the quadratum. The bent structure allows a small turn around the longitudinal axis of the rostral part of the pterygoid, so that the distal part of the quadratum can move dorsalwards, without a dorsal lift of the entire quadratum.

The described construction settles now the position of the joint between quadratum and lower jaw. From the fact that the rostral point of the lower jaw must also lie ventral to the maxillare, and that the maxillare included the poison-fang occupies a determined position and space in the construction, it follows that the line between the joint and the rostral point of the lower jaw cannot lie parallel to the upper jaw. How a parallel course of upper and lower jaws in their rostral part is formed will be pointed out later on.

The rostral, *i.e.* also the most lateral, position of the supratemporale depends on the position of the bony dorsal wall of the statical organ. About the size and the detailed structure of the canales semicirculares in relation to other properties of snakes no data are at our disposal (VAN DER KLAAUW, 1948). The bony wall is about the shape of that of the canales and joins them. The organs of both sides meet almost in the median, leaving only a cavity for a bloodvessel.

There consists probably a mutual influence between the brain and the statical organ. The position of the canales is caudal to the telencephalon, whereas the metencephalon joins the bony labyrinth. The shape of the mesencephalon is influenced by the bony labyrinth. The most lateral position of the supratemporale depends then on the breadth of the bony labyrinth in the dorsal surface of the cerebral skull.

The general pattern of the feeding apparatus requires a more or less special position of the muscles, *e.g.* the musculus depressor runs from the quadratum to the lower jaw and the adductor muscles from the cerebral skull to the lower jaw and from the upper jaw to the lower jaw. The influence on the entire pattern may be called functional, because it is the requirement of a special function which makes it understandable.

Besides the forementioned structures, there are some other ones which are related with the properties of the food. The relatively big prey makes clear the far caudal position of the angle of the mouth, the strong elasticity and the stretching of the tissue in the mouth, and the presence of many glands.

The detailed structure of the members of the components is influenced by numerous factors. In the diagram they are partly indicated. This local influence will be discussed in the following part, where every element will be considered separately concerning its function, position, size and structure.

There are two factors which determine highly the entire pattern, *viz.* the absolute size of the animal and the creeping way of living. Not only has the absolute size an absolute influence on every member, but it determines the position of the elements because it has an unequal influence on the various elements.

The creeping includes a determined height of the cerebral skull. Consequently the relatively big size of the brain means an extension lateralwards. This rather broad shape of the cerebral skull has its influence on the position of the muscles. A detailed discussion on this subject will be given later on.

V. THE DETAILED STRUCTURES OF THE ELEMENTS

A. THE FEEDING APPARATUS

At the discussion of the different parts of the feeding apparatus it must be borne in mind that the apparatus forms a whole, of which the members can hardly be separated. The impossibility of a sharp separation makes a repetition of some remarks now and then inevitable. Sometimes it is impossible to understand the structure of a part but for the knowledge of an allied one. It is obvious that the succession of the parts in the discussion is rather arbitrary.

1. *The muscles*

The rôles played by the muscles in the feeding mechanism are fairly complicated. We do not know exactly the physiological background of the action of every fibre apart and of the muscle as a whole. Generally we may say first that most muscles can contract about 50–60 % of their length in rest (GERGELY & LAKI, 1950), and secondly that every muscle makes the points to which it is attached approach to each other. As for the muscle as a whole the second assumption may give complications if the muscle is a composite one. Finally the balance between the tensions of different muscles makes it almost impossible to determine the share of a muscle in the contraction during a certain movement.

The only thing that may be decided from a morphological fact is that a single muscle can make in a special circumstance a certain movement, or in other words a certain function can be carried out by one or some certain muscles. Next we can try to control the assumption of a cooperation by means of observations. It may be remarked here that a physiological experiment, by activating the separate muscle, can not solve this problem.

In the following part we shall discuss the muscles in succession of their functions in stead of their morphological properties or positions. The reason for this is that the explanation of the problem of the correlation between the forms and functions and the place of the muscles in the whole of the head can be understood easier in this way.

Many authors (KATHARINER, 1900; PHISALIX, 1922; LAKJER, 1926; HAAS, 1931) have given a schematical pattern of the function of the muscles of the head. They all agree that the opening of the mouth, *i.e.* the ventral turn of the lower jaw, is managed by two muscle groups: 1. the musculus depressor mandibulae; 2. the musculus neuro- et branchio-mandibularis. They do not give, however, any other function of these muscles and it is only the combination of these different functions which makes the structure of these muscle groups understandable.

The reason for this hiatus is probably that these authors were not interested in the form-function problem, but only wanted to know which muscle carried out a certain function.

The musculus depressor mandibulae can be divided into two parts. The first part runs from the lower jaw to the median. The contraction of this part gives at first an opening of the mouth and next an approach of the quadratum-articulare joint to the median. This approach is possible by a movement of the supratemporale in such a way that the articulation with the quadratum is moved medialwards and the angle between supratemporale and quadratum is diminished. Together with this movement the quadratum is pushed medio-dorsalwards and so is the caudal part of the pterygoid. This first part of the musculus depressor mandibulae favours the protraction of the old upper jaw. This could be examined in freshly killed animals and with a model.

The simultaneity of a depression of the lower jaw and a protraction of the upper jaw is a necessity in the action of poison injection, where as well the opening of the mouth as the erection of the poison-fang must happen in less than a second.

This part of the musculus depressor has medially a tendinous attachment. The presence of this tendon must be considered as the constructive consequence of a rather strong power concentrated at a small spot. The attachment of this part of the muscle to the caudal face of the lower jaw furnishes a good condition for the farthest opening of the mouth.

The second part of the musculus depressor runs from the lower jaw to the quadratum. It serves for the depression of the lower jaw only. The rostral fibres, ventrally attached to the quadratum, are shorter than the caudal ones, because of the shorter distance available between both places of attachment. Moreover, these lengths of the fibres coincide with their part in the action, because the rostral fibres have to contract over a shorter distance. The contraction of all fibres needs to be only 30 %.

This second part of the musculus depressor has a larger physiological transverse section than the first part. The separation into two parts as well as the relation of their thickness in a transverse section may be considered as a special constructive adaptation to the two kinds of movements required by the swallowing and the injection act. The opening of the lower jaw will require a greater force in the swallowing act than in the injection act, because of the resistance caused by the teeth driven in the prey.

The musculus branchio-mandibularis and the musculus neuromandibularis have most probably a depressive function. It is, however, uncertain in which situation the action of the muscles occurs. The great significance of these muscles may be the depression of the lower jaw during the swallowing when the depressor does not act, namely in pushing the lower jaw ventro-medially instead of a little dorsally.

Generally we may consider the presence of many muscles instead of one strong one as a functional adaptation to various situations in the swallowing act. The development and the differentiation of these muscles is very different in different snakes (LUBOSCH, 1933). The relation to their function is uncertain, because of the lack of knowledge of their shares in this function and the obscurity of the way of food-intake of many snakes. HAAS (1931) assumes that the musculus neuromandibularis plays an important rôle in the peristaltic movement in the pharynx. If the conclusions from his observations are right, it would explain the complex structure of this muscle with two transverse aponeuroses and the branches to the skin and the pharynx. The aponeuroses may permit a separate contraction of the different branches.

The musculus levator pterygoidei, the musculus protractor pterygoidei and the musculus protractor quadrati must be discussed together. The functional significance of these muscles is the protraction of the old upper jaw and the erection of the poison-fang (see LAKJER, 1926, a.o.). The remark of RADOWANOVIC (1928) that the musculus protractor pterygoidei plays an important rôle in the regulation of the depressed position of the poison-fang is most probably right.

The position of the two first mentioned muscles, can be explained by two important factors, which determine the area in which they lie. The rostralwards extension of the area of attachment of the musculus levator pterygoidei is limited by the eye and the joint between the transversum and the pterygoid.

According to LAKJER (1926) an attachment more rostral than the caudal surface of the processus postorbitalis does not occur in the snakes examined by him. This phenomenon can be understood since a levator only occurs in kinetic skulls which have a more or less tropidobasic ventral side. The great space occupied by the eye leaves no room in the orbit for the origin of the musculus levator pterygoidei. The insertion of this muscle is due indirectly to this factor. As a matter of fact there is space to extend on the transversum lateralwards and on the pterygoid rostralwards. The limitation of the area of attachment of the fibres lying most rostrally, however, has a functional aspect. Their course can be directed only ventralward or ventro-caudalward, as the function of the muscle is a protracting or an elevating one. The remark of LAKJER (1926) that sometimes the fibres can be directed rostralwards must be queried. In preserved material with abnormal topographic conditions one gets easily the impression of a course of the fibres against the action direction. Besides it is possible that in a far protracted position of the jaw some fibres may be directed a little rostralwards.

The lateral border of the distal place of attachment near the transversum is also determined by a functional factor. During the rostralward movement of the upper jaw the joint between the pterygoid and the transversum remains at about the same level in lateral projection. The coincidence of the joint with the turning point C in the upper jaw is related to the function of this joint in the retraction of the poison-fang during the swallowing act (see later on). The transversum moves ventralwards, whereas the pterygoid turns dorsalwards (fig. 36). The articular function of the connection between these bones determines vaguely the lateral border of the place of attachment of the musculus levator, because the fibres will not pass the joint, which can be moved ventralwards in a special situation in the swallowing act. Of course this lateral border is not exactly determined by the joint between the transversum and the pterygoid, because during the rostralward movement of the upper jaw the caudal part of the transversum may be turned dorsalwards, followed by a rostralward movement, so that the turning point in the old upper jaw does not coincide exactly with the joint. This makes clear the occurrence of some fibres of the musculus levator attached to the transversum, found in *Lachesis lanceolatus* (LAKJER, 1926).

The coincidence of the turning point and the joint may have a functional significance in the swallowing act. The poison-fang can stay in rest, if the protraction occurs not too far. The cooperation of the musculus levator pterygoidei, the musculus protractor pterygoidei and the musculus adductor pterygoideus can result in a decrease of the angle between the transversum and the pterygoid. The transversum is relatively retracted to the pterygoid, so that the poison-fang is hardly erected.

The extension of the place of attachment of the musculus protractor pterygoidei is difficult to understand as determined by any surrounding element. The places of attachment to the pterygoid of the musculus protractor and of the musculus levator occupy an equal surface.

The position of the rostro-medial border of the place of attachment of the musculus protractor on the cerebral skull is difficult to understand. The places of attachment of the musculi protractores of both sides leave rostro-medially a rhomb-like space between each other. This space is covered with the connective tissue of the mouth-cavity. The extension of this muscle to the median differs much in several species (LAKJER, 1926; HAAS, 1930): generally in the smaller species the median is not reached. Only the hypothesis remains of a close adaptation within the construction of the upper jaw mechanism, namely the fibres have all the same relative length and contract all about 50 % for the most forward movement of the upper jaw. As the relatively bigger cerebral skull in the smaller species has a relatively broader surface in the median and the distances from the pterygoids to the median are relatively equal in different species, this will result in a relatively longer distance between the musculi protractores. All the fibres of the musculi protractores and levatores in a viper have a length of about 6 mm.

In the region of the musculus levator pterygoidei the old upper jaw is elevated over a shorter distance than in the region of the musculus protractor pterygoidei. This more or less transposed position of the muscles in functional sense may be explained as a morphological compromise.

First we may conclude that the fibres of the musculus protractor have a minimum length, for they have to contract about 50 %. This percentage is the limit of power-exertion known for muscle fibres (GERGELY & LAKI, 1950). The musculus levator, which lies near the turning point in the upper jaw, only needs to contract 15 % to give the desired result of protracting and elevating. Suppose both muscles have changed places. Because the shift of the caudal end of the lower jaw is greater than that of the rostral part near point C, the musculus levator should have to contract over a longer distance, whereas the musculus protractor should have to contract over a small distance. The contraction of both would be about 30 %, which is in functional respect rather an advantage than a handicap. The places of attachment would be placed then, however, in the orbita resp. on the supratemporale, which is in the total structure of the head an impossibility.

So we may conclude that the course and the extension of both muscles shows a compromise between the functional requirement and the allowed space.

The musculus protractor quadrati is relatively small. It serves the rostralward movement of the quadratum. The position of this muscle may be determined in the space left between the position of the musculus protractor quadrati and the cerebral skull. The small size of this muscle is in accordance with its function, although no precise relation can be ascertained.

Before a discussion of the muscles drawing the upper jaw back and closing the mouth two situations must be distinguished in which these muscles act:

1. the closing of the mouth without prey, as occurs after the poison injection, when gaping, or after the swallowing act

2. the closing of the mouth with prey, *i.e.* the swallowing act.

In the first case no resistance of any importance occurs; in the second case the resistance is very strong and moreover every part of the head is strained.

In both situations the movements of the bony parts are alike. However, the share of each muscle in each of the acts is not quite determinable. A determination of the working-power or the force of a muscle by measuring its volume or transverse section gives no result by reason of the coordination. Every muscle can contract to a certain degree and thus draw the bony parts into another situation, by which the effective power exercised by other muscles is changed.

It will be clear that for a good understanding of the position and the shape of a muscle in relation to its function one must know exactly the active part played by this muscle.

After all it only remains to discuss the muscles in the same way as we have done at the musculus depressor mandibulae and to sum up some of the possibilities which may occur.

The musculus retractor quadrati draws the proximal part of the quadratum ventro-caudalwards. Probably this movement of the quadratum has also a significance in the forward movement of the upper jaw.

Its small size in *Vipera* can be understood, if the muscle has only a regulating function in directing the position of the quadratum. Such a regulation is very important because of the different phases of the quadratum-movement during the swallowing act.

The occurrence of a tendon must be explained as the consequence of a small place of attachment.

In some snakes (Dasypeltidae; GANS, 1952) this muscle is well developed and serves to slip the lower jaw under the egg.

The big size of the musculus cervico-mandibularis can be understood from its important function of drawing back the upper jaw. The firm aponeurotic attachment is connected with the ligamentum quadratomaxillare, so that the power immediately is transponed on the connective tissue of the glandula venenata. It must be remarked here that the musculus cervico-mandibularis in the viper has neither any morphological connection with the lower jaw, nor any function in moving it.

The musculus retractor palatini must be considered an antagonist of the musculus protractor pterygoidei. The relatively small size of the musculus retractor may be explained by the small space left for this muscle. The place of attachment on the cerebral skull joins that of the musculus retractor vomeris and the fibres lie in a space that is neighboured by the musculus levator. It must be established that the size and the function of the neck muscles and the size and the function of the musculus retractor palatini, which is influenced by the surrounding parts, form one constructive unity. In other words: the small size of the musculus retractor palatini, which is dependent on the surrounding parts, is compensated by the size of the neck muscles (see also the part on the cervical muscles).

The musculus adductor mandibulae externus profundus and the musculus adductor mandibulae posterior help to draw back the upper jaw and adduct the lower jaw. During the contraction of these muscles, which can hardly be separated as well in a morphological as in a functional sense, the lower jaw elevates and after that the angle between the quadratum and the lower jaw is still more diminished, which results in a backward movement of the articulation. The upper jaw is taken along caudalwards with the quadratum.

The whole rostral side of the quadratum and the main part of the caudal half of the lower jaw is occupied by these two muscles. Their relatively large sizes are directly correlated with the way of feeding. The place of these adductores is the only possible situation for adductor muscles in the head of the viper, for in this way they can have an effective result on the elevation of the lower jaw in *every* situation of the jaws. All the other adductor muscles in the viper run to the cerebral skull and therefore come during the swallowing act in an unfavourable position when the upper jaw as well as the lower jaw are moved.

Besides these two important functions the big size is also accountable by the connection of the musculus adductor mandibulae externus profundus with the glandula venenata.

Also from the superficialis-system a great part is unavailable for the adductor function.

The musculi adductores running from the cerebral skull to the lower jaw have all the same function: elevating the lower jaw. Striking is the fact that the adductor system is divided into many separate muscles, running into quite different directions. The explanation of this rather curious situation (realized almost in snakes only) can be found in the fact of a wide opening of the mouth. The lower jaw can move over a large angle and now in almost every position of the lower jaw a muscle is found that runs perpendicularly to the longitudinal axis of the lower jaw.

In consequence of the far caudally situated soft angle of the mouth, which is required by the intake of big prey, the attachment of the muscles to the jaw is also far caudally. The combination of the wide range of movement of the lower jaw and this caudal situation of the muscles explains the curious course, parallel to the lower jaw, of the muscles in rest and the lack of internal aponeuroses. This parallel course and the lack of aponeuroses occur in long muscles which can contract over a long distance. Because there exists an inverse proportion between power and working-distance in every muscle system, the necessary lack of aponeuroses could explain the occurrence of so many bundles in the adductor system in snakes.

Summarizing so far we may state that swallowing a big prey means for the construction of the adductor muscles:

1. displacement of the whole muscular system caudalwards
2. displacement of the strongest power caudalwards in the system
3. dividing of the system into many parts with different courses
4. lack of aponeuroses in long thin muscles.

The way of attachment of the greater part of the adductor muscles must be regarded as a special adaptation to the great movability of the different bony elements. Except the adductores inserting the quadratum, all the adductor muscles have aponeurotic attachments to the lower jaw. Most of these attachments are tangential. This situation allows a contraction of these muscles in almost every position of the lower jaw, which can turn round an axis parallel to its longitudinal axis and move up- and downwards in all these positions. The adductores to the quadratum don't show such a structure, which is in accordance with the fact that the quadratum remains in reference to the lower jaw in almost the same parasagittal plane.

The musculus adductor internus pterygoideus splits rostralwards into three parts, each of which having other functions.

The main part runs from the lower jaw to the transversum, the second part to the connective tissue of the corner of the mouth and the third part, the accessorius, to the caudal part of the pterygoid.

The function of the first part is not quite clear. Haas (1929) assumes that the muscle in *Lachesis* has two functions: first as a retractor of the upper jaw in a fixed situation of the lower jaw, and secondly as an adductor of the lower jaw in a fixed situation of the upper jaw. Though these situations may occur theoretically, one can hardly assume that those functions would be separated. Since the muscle draws the bony parts to each other and the upper jaw as well as the lower jaw are movable, both functions will occur together. Between the elements connected by the muscle are three joints: the articulare-quadratum joint, the quadratum-pterygoid joint and the pterygoid-transversum joint. The articulare-quadratum and the quadratum-pterygoid joints permit no movement, because the axes of the joints lie nearly in the working-line of the muscle force. Except a small decrease of the angle between the pterygoid and the transversum, little motion can occur between transversum and pterygoid. This slight movability and the presence of the muscle make plain the partly or fully retracted position of the poison-fang during the swallowing act. Probably Haas (1929, 1931) also means that the significance of the muscle in the construction is to bridge the more or less opposite actions of the poison-fang in the swallowing and in the poisoning function. The idea of WOLTER (1924) is quite improbable. This author assumes that the pterygoid muscle prevents a turning of the maxillare too far rostralward. Moreover this assumption is based on a wrong determination of the place of attachment.

The place of attachment of the muscle is quite unfavourably situated with regard to the joints between the bony elements; the lever to the force is quite small. This unfavourable situation is compensated by the aponeuroses, which increase the power.

The transversum and the pterygoid can make an angle over and below 180° in a lateral view. In the first case the muscle would be attached to the lower plane of the transversum, in the other case to the upper plane. The constructive consequence of such a different position of the place of attachment must be a tendinous attachment of the muscle to the most lateral point of the transversum.

The second part of the musculus adductor mandibulae internus pterygoideus is an essential element in the function of passing into the rest-position.

The connective tissue in the corner of the mouth is strained between the jaws over the prey. So the corner of the mouth is relatively moved forward. During the closing of the mouth the connective tissue layer in the corner must be drawn caudalwards. This may occur by a contraction of the second part of the pterygoid muscle. The structure of this part of the muscle is simple, except near the attachment to the corner of the mouth. This attachment is aponeurotic and spreads widely in the connective tissue. This construction provides an equal retraction of the connective tissue.

The situation and structure of the musculus adductor mandibulae internus pterygoideus accessorius is difficult to understand. The direction of the fibres allows only a turn of the pterygoid around the longitudinal axis of its rostral part. So a retraction of the pterygoid to the lower jaw cannot occur. The fibres run over the joints between the pterygoid and the quadratum and between the quadratum and the lower jaw. During the injection act the pterygoid is turned around its longitudinal axis by the musculus levator and the musculus protractor pterygoidei, as has been proved in the foregoing chapter. The third part of the musculus adductor mandibulae externus pterygoideus may be the antagonist. The collaboration of the antagonistic muscles may be a regulating function. The precise regulation of the position of the pterygoid by a coordinated function of the musculi protractor et levator pterygoidei and the musculus adductor mandibulae internus pterygoideus accessorius is found in other snakes (*e.g. Dasypeltis*; Gans, 1952).

The group of cervical muscles is well developed. All of them have a large transverse section and show near the area of attachment on the skull surface aponeuroses.

The function of these muscles is the bending of the head and the cervical column and the rostralward movement of the cerebral skull. This double function makes it difficult to prove a strict relation between function and form in these muscles.

The big development of every muscle is mainly to attribute to the function in the swallowing act (fig. 37).

A certain position in the swallowing act shows the jaws moved most rostralwards. The jaws must be drawn now into the retracted position without pushing out the prey. Or in other words, the cerebral skull must be put between the jaws rostralward over the prey. Besides of the musculi retractores, which are less developed, this is the function of the cervical muscles.

Diagrammatically the act may be described as follows:

The head is turned by a bending of the cervical column, suppose to the right. The turning place lies in the rostral cervical region near the occiput (fig. 37a, III, A). Thus the left side of the cerebral skull is moved rostralward between the jaws and the right side is relatively moved caudalwards. Then the left half of the cervical muscles attached to the occiput is contracted, which results in a perpendicular position of the neck on the cerebral skull. After that the neck is bent into some curves more caudalward (fig. 37a, IV). The caudal part of the body being fixed, the neck region can be stretched, which results in a rostralward movement of the cerebral skull. The resistance countering a shoving of the prey is caused by the weight of the prey or by the pressing activity of the ventral cervical muscles.

Sometimes, instead of a rostralward movement of the cerebral skull, the body of the snake is moved caudalwards. During the bending act of the neck the head is moved caudalwards, so that the snake creeps continuously backward during the swallowing act. The swallowing occurs in this case very slowly, or not at all.

Whether a rostral movement of the head or a caudal one of the body occurs depends principally on which share the different parts of the body have in the resistance. The resistance of the head can be varied by lifting it from or pressing it to the bottom. If the jaws and the prey are pressed on the ground then the rostral part of the snake's body cannot move, so that the head is pushed between the jaws.

In other snakes, such as the big Boidae the swallowing occurs almost only by the pushing power of the cervical region (fig. 37b). The jaws are moved rostralwards together with the cerebral skull. The resistance is given by a fixation of the prey with the caudal part of the body.

A collaboration between the cervical muscles, pushing the cerebral skull rostralward, and the musculi protractores, protracting the upper jaw, as exists in *Python*, may occur also in the viper. In that case the protracted jaw can be shifted farther rostralward over the prey by the bending of the head.

The musculi intermandibulares are small muscles, which differ very much in different species (Lubosch, 1933). The function is a contraction of both jaws together. An insight in the relation between the different parts and their functions is lacking. A comparison with the other species (Lubosch, 1933) gives no indications on this subject, because no data of the detailed function are to our disposal.

The problem is quite complex by the unsharp demarcation of the musculi intermandibulares and the muscles to the tongue-bone, in a functional as well as in a morphological sense.

The musculus retractor vomeris is an example of a muscle lying in a very unfavourable situation for its attachments and extension. The function is to draw the olfactorial region ventralwards, for which it must be extended between this region and a fixed point caudal to it. The shortest distance to a fixed point is the distance to the most caudoventral corner in the orbita. The muscle has now to bridge this rather long distance, thereby passing the eye. The short moving distance and the small required power allow a long tendon from the vomer to the venter of the muscle in the ventro-caudal corner of the orbita. In preserved condition the venter has a concave shape.

2. *The bones*

The shape of the bony elements regarded as constructive elements is determined by mechanical and spatial factors. The way of determination is mainly dependent on the relation between the positions of the different elements. Their positions can be considered in correlation with the functions of the elements, or in other words, the positions are dependent on the requirement of the functions.

From this point of view two problems arise. First the correlation between position and function of a certain element, which must be regarded in a larger construction or architecture. Secondly the detailed shape of this element considered the consequence of the constructive influence of mechanical and spatial factors.

Concerning the first problem may be referred to the chapter on the general construction. The second problem, though requiring an exact study, is in principle to be answered. In this chapter the bony elements will be discussed in regard to the second problem.

It must be remarked that the material of which the elements are built generally plays an important rôle in the realization of the function. In the viper there occurs almost only bony material.

The maxillare has an irregular shape and can be divided into a number of structures required for the same number of functions.

The functions are:

1. the bearing of two poison-fangs, which can alternate in function and be shed
2. the articulation with two other bony elements, *i.e.* the transversum and the praefrontale
3. the serving as a place of attachment for some ligaments
4. the placing of bloodvessels and nerves.

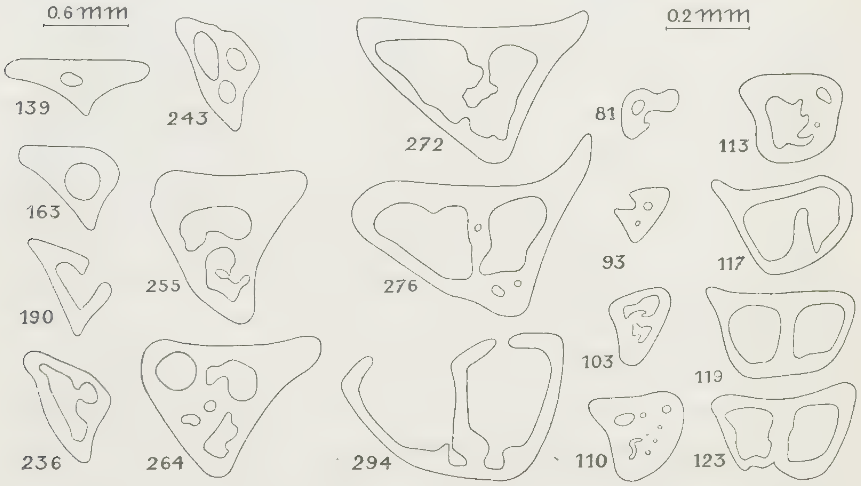


Fig. 39. Transverse sections of two maxillaria from caudal. The figures render the numbers of sections in the series. The left three rows are the sections of the left maxillare of a big animal. The right two rows those of a right maxillare of a small animal.

The structural influence of every functional component may be divided into two factors:

1. the position of the component concerning the problem of the space occupied by it
2. the mechanical or physiological requirements put by the components.

The articulation with the praefrontale, which is found dorsally shows a widening in a latero-medial direction. It is worth mentioning here, that where ever a flat articulation or connection exists between two bones, its surface must be larger than the bones themselves, if the articulation has to resist the same strain as the bone. Supposing the bone has a minimal development in relation to the strain working on it, then it follows that the surface of the articulation must be larger, because the connective tissue of the articulation has a lower resistance to transverse strain than the bone. The connective tissue has less elements per surface unit for the resistance and besides, the flexion of these elements by the shearing strain is greater than that of the compact bone.

The hinge-joint between the maxillare and the transversum is as long as the breadth of the transversum. The breadth of the transversum is correlated with the flexion exercised on it by the muscle strain and the resistance via the poison-fangs, as will be elucidated further on. The caudal surface of the maxillare is flat and bears two transverse ribs, one above the articular surface with the transversum and the other one below it. The breadth of the caudal surface and its flat character is the general shape of the articulations.

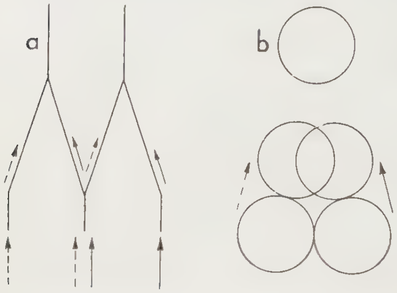


Fig. 40. Diagram illustrating the conduction of pressure of the poison-fang by the maxillare. a, longitudinal section; b, transverse sections on different levels. Further explanation in the text.

Between the articulations, however, a small area is found, where the foramen lies through which the bloodvessels and the nerve enter the maxillare.

As an aid to the resistance to flexion or pressure this flat caudal plane is rather unfavourable.

The strains working on the maxillare are attached to the articular points and the top of the fang. The prey exercises a great strain on the fangs, which can be resolved into strains perpendicular to and in line with the longitudinal axis of the maxillare. Moreover, a high pressure is exerted on the fangs when the prey is seized. In consequence of this we may consider the maxillare inclusive of the fangs as a beam, supported in two points and loaded in the centre. The supporting points are the articulation with the praefrontale and the top of the fang. The loading is a caudalwards drawing of the transversum.

The flexion occurs in a plane perpendicular to the caudal plane mentioned above. Consequently the greatest resistance should be given by a plane perpendicular to this caudal plane. The shape of the surface of moments is about triangular, and the basis is the connecting line between the top of the fang and the articulation with the praefrontale. The greatest moment lies on the level of the articulation with the transversum. We may expect such a shape, that the greatest flexion resistance of the bone lies rostral to the articulation with the transversum. The resistance to flexion can be calculated now from the formula T/W, in which T is the moment of inertia and W the distance from the farthest point in the transverse section to the neutral line. T could be determined by the summation of the moments of inertia (t) of small rectangles perpendicular on the neutral line.

$$t_x = \frac{1}{12} bh^3 + bhx^2, \; t_y = \frac{1}{12} hb^3 + bhy^2, \; t_{xy} = \pm bhxy$$

in which b is breadth, h is height, x is the distance from the centre of gravity of the rectangle to the abscis, y is the distance from the centre of gravity of the rectangle to the ordinate (POHL, 1941; KLOPPER, 1946).

The numbers of the two series of transverse sections of the maxillare (fig. 39) are given in table I.

The calculated surface of the moments of resistance has a regular shape, only one transverse section (110 resp. 255) diverges.

Although the resistance to flexion fits the expected surface of moments in transverse section, the shape of the maxillare does not answer the theoretical form. The main factor inducing another shape is the implantation of two fangs. The base of the fangs must be supported by circular bony ridges in a transverse section. Such a ridge (spatially the transverse section of a cylinder) takes the place of the expected surface that would stand rostralwards on the caudal surface of the articulations. Dorsalwards the circular shape can be quit more or less and is more adapted to a straight surface, *i.e.* in this case a triangular shape.

Suppose the strain in a penetrated position of the fang can be resolved into two equal components, then the stresses of the flexion are almost equal and the component of pressure will be of relatively little influence. Therefore an equal distribution of the bony mass over the transverse section may be expected. However, the strains are conducted through the fangs, which have only peripheral mass, so that generally also a peripheral distribution in the bone is realized. Moreover, each fang works separately and on an other spot. The different time of action of each fang makes it in a constructive sense necessary to conduct the strain through one cylinder for each fang. Only one cylinder is in function to conduct the strain dorsalwards (fig. 40), because only one fang works at a moment. The cylinders stand more or less sloping to each other. The amount of bony mass will be unequal in every transverse section, in that way that near the basis of the fang there will be twice as much mass as in the dorsal part. In the transitional area a somewhat greater amount may be found. The surfaces of the different transverse sections are (fig. 39):

–, 80, 133, 296, 287, 286, 300, 285.
–, –, –, 202, 268, 612, 539, 526, 550, 419.

Nr	B	81	93	103	110	113	117	123								
Maxillare	$W_{x,}$	161	158	345	1142	1180	1642	1532								
(right)	$W_{x,\ \mathrm{min.}}$	115	158	345	1047	885	1095	1022								
Nr	A	163	190	236	243	255	264	272	276	294						
Maxillare	$W_{x,}$	199	396	425	679	3413	2591	3344	3299	2727						
(left)	$W_{x,\ \mathrm{min.}}$	199	396	425	679	2671	1974	2785	3299	2230						
Nr	A	292	300	321	335	357	390	412	432	439	462	471	479	497	542	561
Transversum	$W_{x,}$	858	860	635	393	484	674	458	303	375	498	662	539	618	590	600
(left)	$W_{x.\ \mathrm{min.}}$	674	573	494	344	424	674	379	303	375	498	662	539	618	531	538
	W_{y}	11141	7641	5182	5478	4412	3384	1982	949	719	692	714	697	826	934	945
	W_{x}	710	830	111	125	125	550	666	231	366	510	460	530	590	460	400
	W_{q}	11565	7791	5282	5530	4484	3384	1780	836	530	720	920	780	960	1120	660
Nr	B	291	320	348	357	368	375	386	401	412	422	436				
Pterygoid	W_{x}	362	460	262	222	191	168	233	193	192	168	164				
(right)	W_{y}	—	—	—	186	198	159	192	168	99	123	92				
Nr	B	265	269	303	321	342										
Lower jaw	W_{x}	369	358	387	435	602										
(left)	W_{y}	269	287	320	389	453										

TABLE 1. Numbers of moments of resistance calculated in the transverse section. Further explanation in the text.

The numbers 296 (section 110) and 612 (section 255) are rather high. This is due to the presence of a bony ridge dorsal to the articular surface with the transversum. This ridge cannot have any significance for the resistance to flexion, nor for the pressure, but must be regarded as a block for the transversum.

The ligaments attached to the maxillare resist a strong rostral turn of the maxillare. Their influence equals that of the transversum in the flexion-diagram; they are attached close to the articular surface with the transversum.

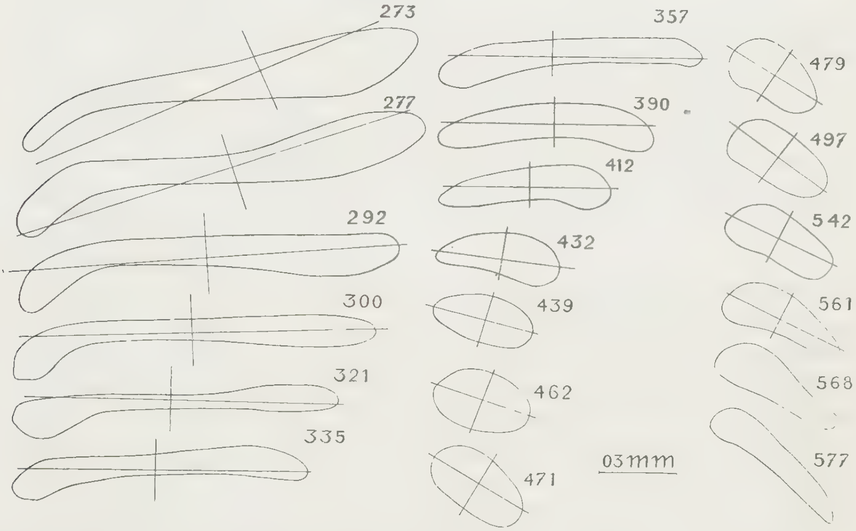


Fig. 41. Transverse sections of the left transversum from caudal. The figures render the numbers of sections in the series. The axes are the main axes of inertia.

The entrance of the nerves and the vessels lies close and ventral to the articular plane with the praefrontale. The foramen lies near the neutral plane in constructive sense, in that way influencing the shape very little.

The maxillare can be explained thus by the integration of the influence of the components from 1–4 (see above). Each of these components may give another shape to the maxillare, whereas at the same time the influence of every component is fully realized. A compromise does not occur. From the forementioned components the first two are the most important ones and they work in two manners, *i.e.* as spatial and as mechanical factors. The third and the fourth component are of relatively little influence.

It must be remarked that in this discussion has been started from the assumption that the realizations of the required structures are minimum phenomena. An argument that such an assumption is plausible is given by the occurrence of extra bony mass around the articulation with the transversum.

In the following discussion on the other bones the same assumption will be used as a starting-point.

The biological background of this minimum phenomenon is unclear as yet.

The function of the transversum (fig. 41) is the transmission of the movement of the pterygoid to the maxillare. This function requires a structure determined by the places where it is placed in between and by the muscles that exercise strains on it.

The way of erection of the maxillare requires a joint which enables the transversum to turn in a parasagittal plane. Moreover, this joint must be a hinge, thus preventing a turning into a lateral direction.

The length of the axis of this hinge-joint is dependent on the breadth of the transversum. This breadth is primarly determined by the requirements of the flexion exercised on the transversum. The presence of both fangs is of little influence, because the neutral line to flexion lies most favourable just between both fangs.

The protraction is caused by the musculus protractor pterygoidei and the musculus levator pterygoidei. Both muscles have their working-line resp. medio-rostralward and medio-dorso-rostralward. Since the muscles are attached to the pterygoid and this bone is connected with the transversum with a broad, firm articular surface, it is possible to divide the muscle strain into three components, one working rostralwards in the neutral line of the transversum, and the other ones in two planes perpendicular on it. The rostral component gives a small pressure, because at the start of the protraction the maxillare is turned. The dorsalwards directed component has hardly any influence on the strain (table I, Wx). The hinge-joint has some friction indeed, but this is of little influence. The component directed medially raises an important flexion (table I, Wy). In this direction almost any movement of the transversum is prevented. Consequently the entire medial component causes a flexion that increases rostralward. A triangular flat bone resists exactly this flexion. The mass division in transverse section, however, is unequal. This is due to the simultaneous influence of flexion and pressure. The flexion causes medially a pressure and laterally a tension. Besides, the small pressure exercised by the component directed rostralward must be added to it, so that the medial part must have a little more bony mass than the lateral side.

The contraction of the musculus adductor mandibulae internus pterygoideus causes a pressure in a caudal direction and flexions in a lateral and a ventral direction. The flexions increase caudally. The shape of the transversum fits these strains, it is rostrally a narrow plane, caudalwards changing into a more or less round bone.

The musculus adductor mandibulae internus pterygoideus is attached to the very latero-rostral point of the transversum. Consequently a turn round a dorso-ventral axis in the joint is made. The influence on the structure of the bone is small, because the transversum is relatively long.

Another consequence of the lateral attachment of this muscle is the unequal spreading of the pressure of the caudalward component. It causes along the lateral side of the bone a high pressure stress, which spreads caudalwards over the whole breadth. Added to the stresses caused by the flexion, the bony mass will mainly be situated laterally.

The influences of the muscles working in opposite directions can be added now. If doing so, one must realize, that the activity of the systems is non-simultaneous, so that the structure serving for the resistance to the strains in one direction, also must be taken into account for the resistance to strains in the opposite direction.

The shape of the bone must be rostrally a plane in a latero-medial direction, changing caudalwards gradually into a narrower, somewhat higher bone and becoming most caudally more or less circular in transverse section.

The bony mass in the rostral part is mainly located near the side, whereas the circumference of the neutral line is thin, because of the unequal position of the strain over the transverse section.

This theoretically deduced shape is quite in accordance with the shape of the transversum of the viper.

The described situation only shows a general trend. This trend is demonstrated in table I, where the calculated moments of resistance are given. The resistance to the dorso-ventral axis (Wy) is rostrally high, caudalwards it decreases. The most caudal part shows a somewhat higher resistance. The resistance to the X-axis is very small. The calculated resistance to the main axes is of less value, since the strain is not exercised in their planes. A turn of the main axes at a fixed position of the transverse section (*i.e.* the natural position) shows the same trend (fig. 40). The transverse sections in the region of the articulations are determined by other factors.

The articulation with the pterygoid has the shape of the last transverse section of the non-articular part of the transversum. It is somewhat broadened, which is due to the difference in mechanical resistance of connective tissue and bone, as is pointed out in the chapter on the maxillare.

The supporting point for the transversum and the pterygoid during the swallowing act lies in that part of the pterygoid which bears the teeth. Moreover, in a special position the pterygoid is fixed caudally by the ligamentum quadrato-pterygoidale. At the start of the protraction the part of the pterygoid lying caudal to the transversum, may be considered a beam supported at the rostral end. It is obvious that during the erection of the maxillare in the swallowing act the pterygoid together with the transversum must be considered as one beam, turning on the hinge-joint of the transversum with the maxillare. At a second stage of the swallowing act the caudal part of the pterygoid must be regarded as a beam supported at its two ends, *i.e.* the rostral part of the pterygoid and the ligamentum quadrato-pterygoidale.

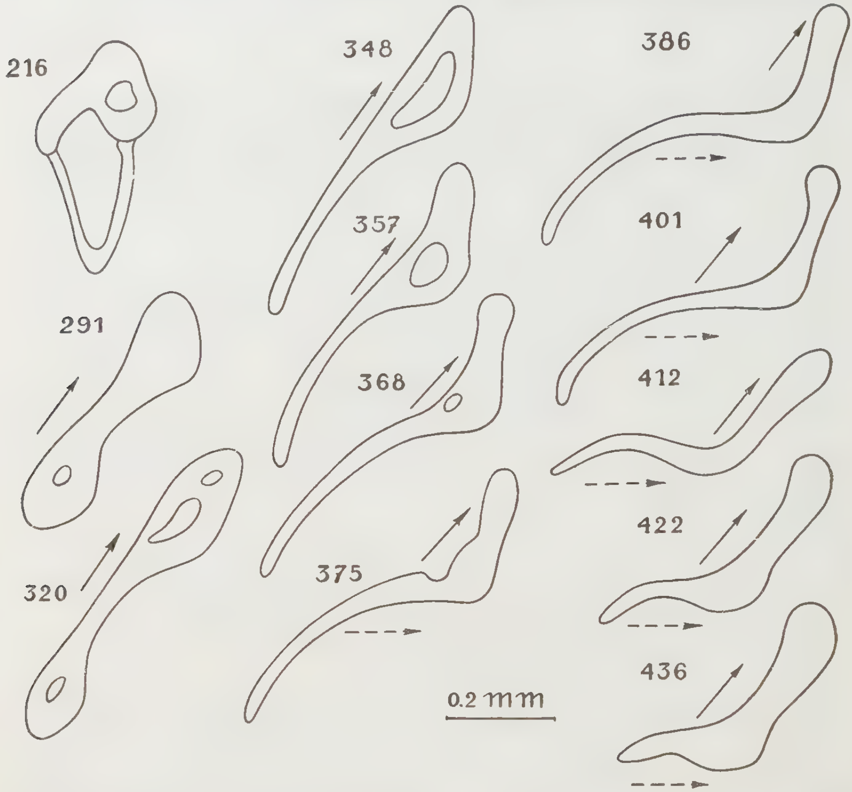


Fig. 42. Transverse sections of the right pterygoid from caudal. The figures render the numbers of sections in the series. The traced arrows indicate the course of the fibres of the musculusprotractor pterygoidei and the musculus levator pterygoidei. The broken arrows that of fibres of the musculus adductor internus pterygoideus accessorius.

Although at all stages of the swallowing act a movement of the pterygoid occurs, the pterygoid may be considered as a beam in a static position, because of the great resistance given by the prey.

At different stages in the swallowing act the influence of the muscle strain is of a different character.

At the first stage the flexion is greatest close to the supporting point near the rostral part and decreases caudalwards. Moreover, the influence of the musculus protractor is in this respect of less importance than that of the musculus levator. The flexion will occur in the direction of the course of the fibres, because a neutralisation of an influence in any direction does not occur by the presence of a joint.

At the second stage of the swallowing act the greatest flexion happens at the place of attachment of the musculus levator, it is somewhat less at the place of attachment of the musculus protractor. Towards both ends of the beam the flexion decreases apparently.

A rough addition of the resistance to the influences at both stages gives a flat bone with its greatest extension at the rostral part of the place of attachment of the musculus levator, *i.e.* near the connection with the transversum.

The great increase of the resistance against flexion rostrally is realized by a thickening of the lateral side of the pterygoid (fig. 42), instead of a plate-shaped extension. The greater part of this thickening is lengthways transfixed by a canal containing bloodvessels and nerves. Probably, however, this thickening is mainly due to the partition of bony mass in relation with the mechanical factors, instead of to the presence of bloodvessels and nerves. The direction of the muscle fibres and thus the direction of the force is latero-dorsally, a little rostralward. Consequently in the latero-dorsal part the flexion and the pressure work in the same direction, whereas in the medio-ventral part the pressure partly compensates the flexion.

Caudalwards the transverse section of the pterygoid is composed of two wings making an angle of about 120° with each other. This complicated situation is due to the presence of the musculus adductor internus pterygoideus accessorius. Each wing is directed in the direction of the muscle strain of one of the muscles, forming a maximum resistance against flexion. Suppose the muscles do not work simultaneously, then each wing plays a part in both flexions. The wing which is situated in the direction of the course of one muscle is practically the main resistant factor to that muscle strain. In theory there are four possibilities of placing the two wings together. The necessary place of attachment for the musculus protractor pterygoidei which runs into a latero-dorsal direction makes a latero-dorsal connection of both wings in a constructive sense improbable. In a ventrally connected situation the medial direction of the wing to which the musculus accessorius is attached is plausible by the fact that an abrupt transition from the caudal structure into the rostral structure is constructively impossible. This wing is directed medialwards, so that the place of attachment of the musculus levator can be extended on the dorsal surface of this wing. If the wing should be directed lateralwards then an abrupt transition to the opposite direction should be necessary for the extension of the musculus levator. A connection of both wings medio-dorsally does not occur, which can be understood from the assumption that in mechanical and in ontogenetical sense a connection of both wings far from the primary part of the pterygoid is impossible. The calculated moments of resistance (table I, Wx in the direction of the force of the musculus protractor, Wy in the direction of the musculus pterygoideus accessorius) show a regular increase from caudal to rostral. Between section 386 and 375 a remarkable decrease is found, whereas it increases rostralward more than before. This difference in increase and the hiatus are due to the part serving for the resistance to the musculus pterygoideus accessorius. The moments of resistance, which can be expected for the strain exercised by the musculus protractor pterygoidei, will gradually increase from caudal to rostral. The moment of resistance to the strain of the musculus pterygoideus accessorius is almost equal for the whole distance (with a small maximum in its centre) over which it is attached,

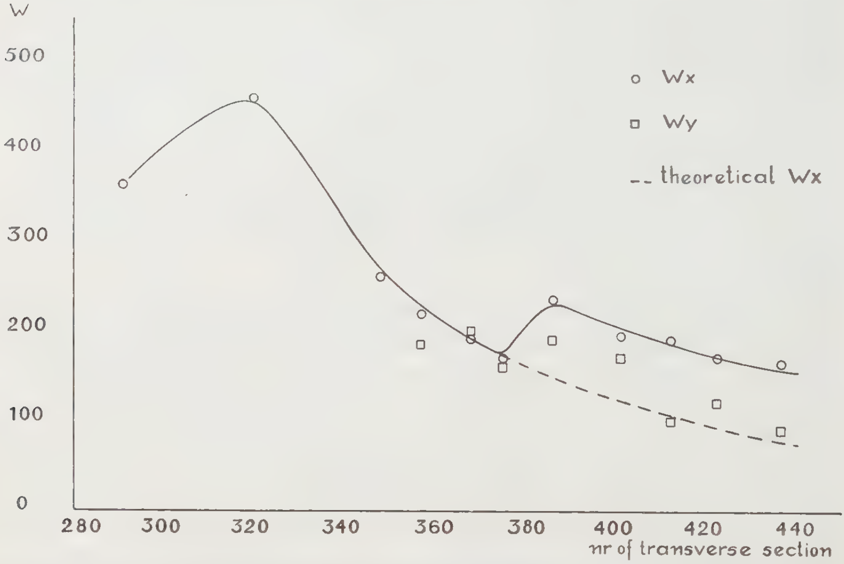


Fig. 43. Diagram of the surfaces of moments of resistance of the caudal part of the pterygoid.

for the pterygoid may be considered a beam supported at two points, if the muscle contracts. One point is formed by the ligamentum quadrato-pterygoidale, the other one by the supporting of the pterygoid on the prey. The direction of the moment of both resistances is different. If both moments of resistance can be taken into account for each strain, one being greater than the other, then each moment would be increased gradually from caudal to rostral. The moment of resistance for the musculus accessorius is considerably smaller than that for the musculus levator. The surface of moments would have the shape of that of the resistance to the strain of the musculus levator pterygoidei. The moment of resistance does not increase gradually, which is due to the influence of the wing to which the musculus pterygoideus accessorius is attached (Wy). The moment of resistance to the strain of the musculus accessorius can be derived from Wy. This number must be diminished with a number caused by the resistance of the wing for the musculus levator. This wing will have a small resistance in the Y-direction, because its main extension lies almost perpendicular to the Y-direction. It shows a gradual increasement of its resistance rostralward.

If the moment of resistance for the musculus levator increases gradually from caudal to rostral, then the increasement of the calculated moment of resistance in the caudal part of the pterygoid in regard to its centre part is due to the influence of the wing for the musculus accessorius (fig. 43). Both resistances are realized by adding, not by integration.

The inplantation area of the teeth passes caudalwards the articulation with the transversum. The functional requirement needs a placing of the teeth on the ventro-medial side. This situation is just contrary to the mass partition in these transverse sections. Consequently an extra strengthening is necessary. The strains exercised on the teeth are distributed equally. The directions of the strains lie perpendicular to the bone and in its longitudinal axis. The strains result in a normal and a transverse pressure and in a flexion. The resistance to these strains is proportional to the surface of the transverse section. The flexion is relatively quite small by the very short lever. A certain outer shape cannot be derived only from the proportion between the pressure strain and the surface of the transverse section. This is the case with the pterygoid in the part rostral to the joint and in the area of the joint itself. Only the extension or the mass of bone is related to these influences. The outer shape is probably correlated with the presence of an articular surface and the implantation of the teeth.

The quadratum is connected with two joints. Consequently hardly any flexion will occur, because the strains in almost every direction will result in a movement. The greatest strain will be exercised by the musculi adductores profundus and posterior, when the prey is swallowed in.

In accordance with the muscle strains the quadratum is a rather narrow bone, somewhat flattened in the plane of the course of the muscle fibres. The detailed shape of the quadratum cannot be derived from the strains exercised by the muscles, since the share of every muscle in the strain diagram is unknown.

The upper and lower end of the quadratum form the two joints.

Generally the shape of a joint is mainly due to the requirements of moving. The constructive requirement for the joint with the lower jaw is the possibility of a high degree of movement in a parasagittal and in a transverse plane. The movement of the lower jaw in the parasagittal plane must be able to occur in every position of the quadratum. The quadratum moves as well into a rostro-caudal as into a medio-lateral direction. The consequence for the joint is to be a construction which allows a turn of the lower jaw round its longitudinal axis. The joint which permits flexion, extension, ab-and adduction and circumduction is realized in the saddle (*cf.* WELLS, 1951). All these terms are used in a dynamic sense.

The pressure exercised on the inner surface of the joint stands as good as perpendicular to this surface. Suppose the pressure is equally spread all over the surface. Then the flexion (in mechanical sense) requires a knob, of which the position of the outer surface is dependent on the tension.

The way of moving of the quadratum requires on the quadratum a lateral and a medial knob, on the lower jaw a rostral and a caudal one. The more or less lateralward directed position of the distal part of the quadratum, together with the articulation with the pterygoid result in a small difference between the medial and the lateral knob. The outer surface of the medial knob is somewhat flatter.

The area between these knobs serves as an articular knob in the joint cavity of the lower jaw. Here occurs only a pressure, which is directed inwards.

The joint with the supratemporale serves for the caudo-rostralward movement of the quadratum. Only a small movement into a lateral direction is useful. Out of many possibilities one of the simplest is realized. The top of the quadratum occupies laterally a flat area on the supratemporale. The upper part of the quadratum is flattened. The capsule of this joint is very loose.

The supratemporale needs only to resist a strain in a medio-dorsal direction. It is flattened in the plane of the direction of this strain. The directions of the strains exercised by the musculus adductor mandibulae externus medialis and the ligamentum parieto-supratemporale lie in the same plane. It must be remarked here that no pressure and hardly any flexion occur, because of the ligamentous transmission of the strains. The influence of forces will result in a movement and the remaining strain will be spread over the skull by the ligaments. Only in the caudal part appears some flexion when the bone stands in the most medial or the most lateral position and the strains on the quadratum endure. In relation with this fact the sharp-pointed caudal part must be considered. The small sharp-pointed extension occurring sometimes on the lateral ridge can be understood as a place of attachment of the ligamentum supratemporale-glandulare.

The lower jaw has a complicated structure. In functional respect it may be considered as a unity when serving for the swallowing act. Nevertheless the possibility exists of a division into a number of functional components. The connection of these components can be found in a rod, which is, when they are used simultaneously, here called: the lower jaw itself.

The components are:

1. the joint with the quadratum
2. the part serving for the attachment of the muscles
3. the part bearing the teeth
4. the area serving for the attachment of the ligamentum intermandibulare
5. the space occupied by nerves and vessels.

The position of the lower jaw is dependent on the position of the articulation with the quadratum and on the position of the rostral point of the lower jaw. In the former chapter the conclusion could be made that the position of the lower jaw comes up to the constructive requirements of the elements of the upper jaw.

There is no constructive reason for a bent rod, unless the lower jaw must run parallel to the upper jaw. If the last mentioned condition must be realized, then a bent caudal part of the lower jaw is the best construction.

The biological significance of a bent jaw is important. Same as in the pterygoid, the caudal part of the lower jaw can be moved lateralwards, without a displacement of the rostral part. This phenomenon happens when the lower jaw is turned around the axis of its rostral part.

The detailed shape of the jaw can be understood by dividing it into the components mentioned above.

The lower jaw moves over variably long distances in the swallowing as well as in the poisoning act. The greatest distance is covered by the rostral point, the more caudally lying parts move over shorter distances.

The quite variable position of the lower jaw makes the influence of the surrounding components different in the different phases of the acts mentioned.

During the swallowing act the jaw may be considered as a beam supported at both ends, *i.e.* resp. the rostral teeth bearing part supported by the prey, and the caudal part supported by the quadratum. At the start of the swallowing the construction is labile, that is to say when forces are exercised on it, the jaw will start moving. For all that the construction can be looked upon as a statically determined one in a farther closed position of the mouth during the swallowing act.

The loading on the jaw is made by the muscles, the reactions are given by the prey and the quadratum. The muscles running from the cerebral skull may pull from different directions and at different angles in an almost parasagittal plane. The caudal muscles run from the quadratum and consequently pull in an almost fixed position, because of the same position of the quadratum with regard to the lower jaw in the different phases of the act.

The muscles cause a flexion, a transverse strain and a normal strain on the bone. The assumption of HAAS (1931) that the lower jaw has only to resist a normal strain is wrong, because the muscles are attached to the lower jaw in such a way that they stand almost perpendicular on the longitudinal axis. The normal strain is very small because of the almost perpendicular attachment of the muscles. The transverse strain is greatest at both supported spots, but is of little influence compared to the flexion.

The greatest flexion is found in the area of the rostral fibres of the musculus posterior. With respect to an equal distribution of the strain over the bone the maximum flexion lies rather caudally, because the muscle fibres are unequally divided over the entire area of the different places of attachment and the greatest amount of muscle fibres lies in the caudal part.

The resistance of the various parts of the jaw must be in accordance with the flexion if a minimum amount of bony mass is present. This fact is proved indeed. In the rostral part the jaw is almost annular in transverse section (fig. 44), thus giving resistance to different directions of muscle strains. Caudalwards the annular shape disappears, and really the flexion resistance has increased (table I). The non-annular shape here is probably due to the entrance of the nervus trigeminus. The coincidence of the entrance of a nerve and the increase of the flexion resistance ought to be correlated with quite a big jaw, if it is annular in transverse section. The fixed direction, however, of the muscle fibres to the jaw in this area allows a plate-shaped extension. An argument that the muscles do not induce in constructive sense the plate-shaped extension, lies in the fact of the attachment of the musculus pseudotemporalis to the rostral part of this extension. The direction of the musculus pseudotemporalis to the lower jaw differs considerably during the swallowing act, so that in this area also a cylindrical lower jaw could be expected, if only the muscles would induce the shape. Moreover, the fibres of the musculus posterior and the musculus profundus are not attached to the whole area of the extension.

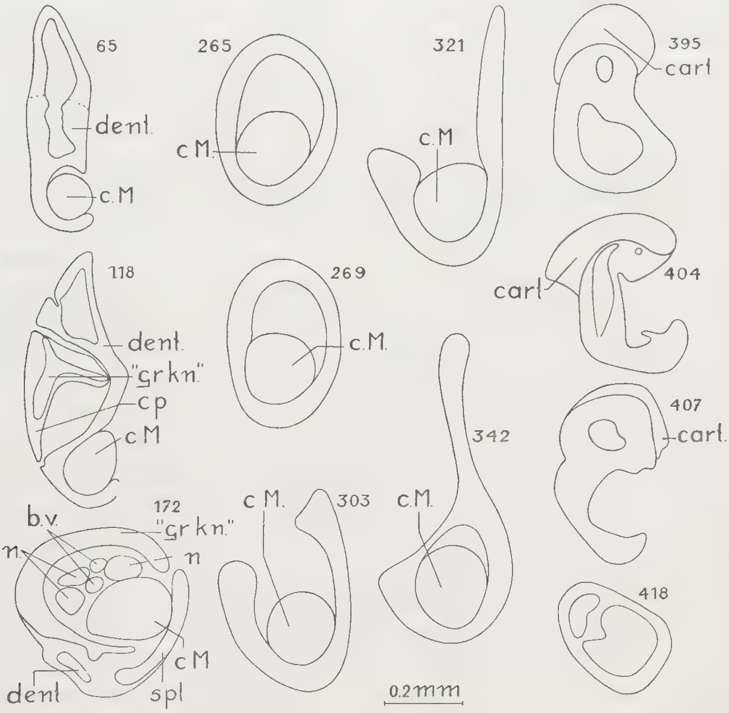


Fig. 44. Transverse sections of the left lower jaw from caudal. The figures render the numbers of the Sections in the series. *b.v.*, bloodvessel; *c.M.*, Meckelian cartilage; *c.p.*, cartilaginous part of the "Groszknochen"; *cart.*, cartilage of the joint; *dent.*, dentale; "*gr.kn.*", "Groszknochen"; *n.*, nerve branches; *spl.*, spleniale.

The plate-shaped extension cannot be correlated with the required mechanical resistance at a later stage of the swallowing act. In every further backward position of the prey the flexion will be less than at the start of the swallowing, because of the loading which lies over the whole length of the jaw, the greater part lying in the caudal half. So in every position of the prey the surface of moments lies within the surface of moments for the entire jaw.

Assuming a precise adaptation to flexion of the bony mass in the transverse section several possibilities exist for the construction of a jaw with an annular transverse section. The same flexion resistance as occurring in a massive circular section can also be realized by a ring with a great radius. But the greater the radius the smaller the surface of the bone in the transverse section. On the other hand the surface of the bone in the transverse section cannot decrease below a determined extent, which is dependent on the size of the transverse strain and the pressure. The realization of a precise adaptation to both these strains and the flexion is to depend now on the resistance of the bony material against these strains.

The annular shape of the transverse section of the lower jaw is not maintained in the teeth bearing part and in the parts ventral and caudal to the joint.

Between the rostral teeth bearing part and the area of muscle attachment lies a rather loose intermediate part.

The rostral part, bearing the teeth, consists rostrally of two parallel bony plates, running into a dorso-ventral direction. These lateral and medial plates are connected on three places: ventrally, dorsally and halfway between. This structure is coherent with the direction of the pressure exercised by the prey. This pressure is mainly exercised on the teeth and partly on the medial side. The flexion and the transverse strain work by means of the teeth in the plane of the greatest extension of the jaw, that is the direction in which the teeth are placed.

Caudalwards the pressure on the medial side increases—the teeth are directed more medialwards and the prey lies at this stage between the jaws—which must give rise to a strengthening in a latero-medial direction, realized in the connecting plates. More caudalwards the area with a dorso-ventral resistance must change into an area with resistance in many directions, the annular transverse section. The intermediate part, however, is rather more complicated than would be expected.

Together with the change of shape a change of bony elements happens. The dentale is transplaced by the "Groszknochen". The lateral plate of the dentale disappears and the medio-lateral connections become firmer. The incisura in the lateral plate of the dentale is filled up by the "Groszknochen". The middle connection in the dentale disappears and the "Groszknochen" becomes T-shaped in transverse section, *i.e.* a long rod in a dorso-ventral direction and a smaller one in latero-medial direction (*cf.* fig. 44, section 118). Caudalwards the dorsal part of the T-shaped bone disappears and the remaining parts grow circular. In this intermediate area the medial plate of the dentale disappears and is replaced by the small spleniale, which is caudalwards firmly connected with the "Groszknochen" by connective tissue. In the medial fenestra is also a loosely connected element, the angulare, according to Versluys (1936).

Mechanically this construction is unfavourable in many respects, only a tension can be resisted. According to Versluys (1936), referring to Conybeare and Buckland, the lot of elements would give a favourable mechanical resistance. Indeed, this holds good if the elements are situated parallel to each other and so constitute a simultaneous resistance in a certain direction. The loosely connected elements are, however, placed in series giving hardly any resistance to flexion nor to pressure.

The functional or biological significance of the weak intermediate part is the same as that of a joint. The rather strong movability in lateral direction and the small one in ventral direction permit a bending of the rostral part in these directions. The pressure on the prey by the adductor muscles is lowered and a flexion, as would take place in a firm rod, does hardly exist.

The presence of two separate small elements, the spleniale and the angulare, cannot be explained from this. We may assume that this structure can be regarded as an ontogenetic or phylogenetic one, upon which no or hardly any mechanical demands are made.

The area ventro-caudal to the joint shows a peculiar structure, influenced simultaneously by three components: the joint, the musculus pterygoideus and the musculus depressor.

In principle the joint has the same shape as that on the quadratum. It is, however, fully incorporated by the other structures of the lower jaw, so that the outer circumference does not show a spherical shape. It is rostrally continuously connected with the plate-shaped extension, which can give the same mechanical resistance. Laterally and medially the outer spherical shape is more or less present. Caudally it disappears partly into the processus retro-articularis. Ventrally the outer circumference does not occur. The ventral surface of the lower jaw coincides with the outer surface of the joint.

Between the inner and outer surface of the joint a connection is made by a parasagittal bony plate. This varied construction is correlated with the entrance of a nerve and bloodvessels. The opening for these elements in the lower jaw lies in the medial surface ventral and caudal to the joint and consequently the entrance in the cavity ventral to the surface of the joint gives rise to a connection of this cavity with the outer circumference. The mechanical resistance of the medial part of the joint is decreased strongly. The bony parasagittal plate in the middle of the jaw may be regarded therefore as a strengthening of the joint, as a consequence of the entrance of nerve and vessels.

The second consequence of the existence of this opening is the place of attachment of the musculus pterygoideus. The attachment is limited to the ventro-medial side, thus ventral to the opening. A thick part of the lower jaw is correlated with this attachment. The direction of the strain during the swallowing must lie in almost the same direction as the longitudinal axis of the jaw, for the fibres are attached almost tangentially. It seems plausible to consider the thickened ventro-medial ridge as a resistance to the pressure.

Caudal to the joint the dorsal surface is occupied by the area of attachment of the musculus depressor. The constructive influence here is for us uncertain. The construction is, in relation to this muscle influence, in mechanical view statically undeterminable. However, there will probably occur hardly any flexion, because of the short lever between supporting point and place of attachment of the muscle fibres. Since the fibres are perpendicularly attached to it, only a transverse strain influence perpendicular on and a pressure influence on a plane parallel to the dorsal plane can be expected. These strains may be an explanation for the trabeculae which occur in the direction of these strains.

Generally the shape of the lower jaw can be understood by the constructive properties required by the surrounding parts. Many detailed structures remain unexplained, though. This may be due to four factors:

1. the strains caused by the different muscles are considered strongly diagrammatically; the strains are considered for ideal situations, and this does not hold good for curved surfaces of an irregular shape and with foramina
2. in many cases the integration of components could not be elucidated
3. in the consideration of the structure is not or hardly reckoned with the elasticity of bone and cartilage
4. the processes of growth and demolition complicate the structure.

Between the discussed structures of the lower jaw remains plenty of room. The greater part is occupied by nerves and vessels. The rest is occupied by the cartilage of Meckel (fig. 44), running from rostral in the dentale to caudal in the processus retro-articularis, interrupted by the joint. The function of the Meckelian cartilage at the adult stage is unknown. In mechanical respect it is unimportant. If it has any function it is the elasticity in the intermediate area. It is more plausible, however, that this cartilage has no function at all at an adult stage. It may be an ontogenetical structure that has lost its function. The lack of knowledge of functions of ontogenetical structures makes it impossible to give any valuable remark on this point.

3. *The teeth*

The curved shape of the teeth cannot be understood from a mechanical point of view. Indeed, the flexion is decreased by the curved line of the tooth, but on the other hand the total amount of material increases relatively. The realization of the same distance from the basis to the tip of a tooth results in an increasement of the amount of material in the curved tooth compared to the straight one. Comparing their lengths the curved tooth is mechanically a more favourable construction.

The small teeth on the lower jaw, the palatinum and the pterygoid are a little curved caudalward. The function of the curved teeth is important for the holding of the prey. A movement of the jaws in regard to the prey parallel to these jaws will result in a movement also perpendicular on the jaw, so that the teeth are pushed further in.

A special complication is originated in the position of the poison-fang. This tall tooth shows about the same curve as the small teeth. Only the tallness requires a possibility of a turning of the tooth. This movability of the tooth and its curved shape are correlated now in a curious way.

First a curved tooth can be considered as a consequence of the movability. At one hand the fang must be bent in such a way that the sharp point does not project into the closed mouth-cavity. The distance between the articular surfaces on the maxillare prevents a turning of a straight fang far enough. In a curved fang the point shall not project, even if the turn is small.

On the other hand a curved fang allows a necessary closing of the mouth with a retraction of the maxillare, if the direction of the injection of the fang must keep the same angle with the jaw.

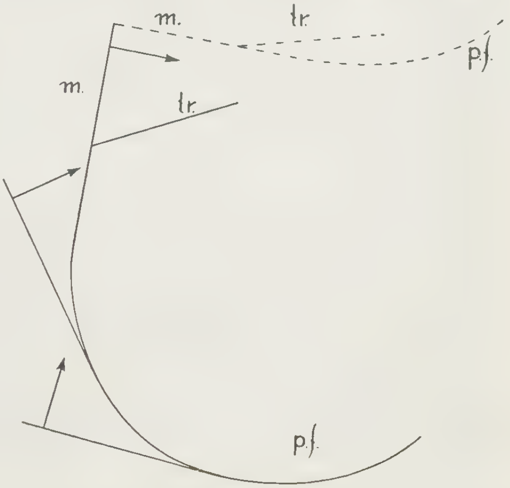


Fig. 45. Diagram showing the different positions of the maxillare, when the poison-fang is pushed into the prey along its axis. The broken line indicates the rest position. The arrows render to the direction of the head, if the maxillare should be immovable. *m.*, maxillare; *p.f.*, poison-fang; *tr.*, transversum.

Secondly the movability may be regarded as a consequence of the curved fang. During the injection act the fang will follow the line of its own curve (fig. 45). If the direction of the body of the animal does not or scarcely change, or in other words, if the animal will not be turned round, then a retraction of the fang must be possible, so that the fang describes a line of its own curve. The entire animal, however, will be moved rostralwards during the injection act.

In fact this situation means a considerable decrease of the flexion on the fang.

From this may be concluded now that both constructive properties (the curved fang and its movability) are adapted to each other, or in other words that both properties show a constructive totality based on a necessary long poison-fang.

According to KLAUBER (1939) the curve of the teeth should be correlated with the way of biting. KLAUBER does not mention a relation between the movability of the maxillare and the size and curve of the tooth. Such a relation does exist, though (compare *Crotalus*, *Bothrops* and *Naja*; KLAUBER, 1939). The fact that big snakes have relatively taller teeth, which are thicker walled, is probably due to the fact that these teeth must mainly resist a flexion instead of a pressure.

The greatest flexion takes place at the base of the tooth and here lies the attachment to the maxillare, which is relatively weak. It happens frequently that the fangs are broken off during the injection act and the small teeth during the swallowing act. The broken fang is replaced within a short time by its neighbour (theory of TOMES; KLAUBER, 1939). A considerable amount of different developmental stages is found in a bag medio-ventro-caudal to the fang. These stages of tooth development are arranged alternately. As is shown the occurrence of shedding has a relatively great influence on the structure of the bone. The same situation holds good for the shedding of the small teeth.

The places of the teeth in development lie at different sides from the adult teeth. The young poison-fangs are situated between the adult one and the transversum, the young teeth of the palatinum and the pterygoid lie lateral to the adult row and those of the dentale are arranged medially. In every case, however, the young stages lie in the best protected situation.

The shedding of teeth at adult stages is closely related to the acrodont situation. In cases of a thecodont implantation the chance of a break-off is more remote.

4. *The nerves*

The course of the nerves innervating the jaw system (figs 32, 33 and 34) must meet the requirement of the large movability of the parts.

The course of a nerve is determined by its origin and the innervated area. Generally the origin will not be changed, but the area of innervation can be moved considerably. This movement in the innervated areas is most extensive at the lower jaw and the connected parts, it is less at the upper jaw.

The jaw and the surrounding parts are innervated by the nervus trigeminus and the nervus facialis. The branches of both nerves have the length of the distance between the origin and innervation when the mouth is widely opened. In a closed position of the mouth the distance is considerably diminished, so that the nerve must be retracted by elasticity or be twisted. Whereas no nerve can be contracted by elasticity, the second way is realized. The ways of twisting differ much and are highly dependent on the extent and the direction of the movement.

The greatest movement of the innervated area is found for the ramus mandibularis nervi trigemini. In the most opened position of the lower jaw this branch lies in an almost straight line from the origin to the entrance in the lower jaw. In closed position of the mouth the nerve is curved. Close to the outlet in the cerebral skull, where the course is changed from ventral into caudal, it has a sharp curve. After running a short distance caudalwards, the nerve curves ventralwards and then runs gradually rostralwards into the canalis primordialis. A most remarkable fact is that the parts of the nerve that are situated near the foramina keep the same position in every phase of the movement. Or in other words, the nerve will never get into contact with the bony ridge of the foramen. In the low and perpendicularly situated lower jaw it must as a matter of fact enter gradually. The consequence of such an entrance is a long foramen and a rostral course of the nerve. The constructive influence of a long foramen on the construction of the lower jaw is discussed above.

The ramus mandibularis branches off some smaller nerves, which innervate the musculus adductor, the tissue around the teeth and the teeth themselves, the floor of the mouth-cavity and the glandulae labiales. These innervated elements are not movable with regard to the lower jaw, so that the diameters of the foramina for these nerves can be equal to the diameter of the nerve-branches. The foramina are circular.

A number of branches of the nervus trigeminus splits off close to the origin. These branches innervate the muscles. The movement of these innervated areas is less than that of the lower jaw, though still considerable. The branches of which the main part has been described, run between the muscles in short twistings. The curves differ in several branches, but the general pattern is the same.

It is uncertain which factors determine precisely the peculiar curving of the nerves.

The ramus maxillaris is influenced to a less degree by the jaw apparatus than the ramus mandibularis. The curves are smaller. In the neighbourhood of the ductus venenatus are some curves, directed rostralward in a closed position of the mouth. The connective tissue around the gland and the ductus is stretched during the injection act, so that the nerve is stretched too.

The ramus ophthalmicus superficialis shows no curves at all. In its area no or hardly any movement happens.

The nervus facialis runs almost straight to the musculus depressor mandibulae, along the columella auris. The columella runs from the fenestra ovalis to the centre part of the quadratum. With a latero-rostral movement of the quadratum the distance between the fenestra ovalis and the centre part of the quadratum varies very little.

The nervus glossopharyngeus and the nervus vagus must bridge a quite movable corner of the mouth to reach their innervated areas, of which the positions change much. Both nerves are curved spirally close and caudal to the corner of the mouth, in such a way that on a very small spot a very long nerve band is situated. Close to the tongue the glossopharyngeus lies also in spiral-shaped twistings. Moreover, the four branches of the nervus glossopharyngeus run rostralwards, bend caudalward and innervate the tongue muscles far caudally. In the most forward position of the tongue these branches are stretched.

Generally the nerves are just as long as is required by the greatest distance to be bridged. It was possible to show this in freshly killed animals and preserved ones. Only the lengths of the nervus glossopharyngeus and nervus vagus around the corner of the mouth could not be exactly determined. Probably the extension of the mouth-cavity during the swallowing act plays an important rôle in the determination of the distance to be bridged.

5. *The bloodvessels*

The great elasticity of the bloodvessels makes any special construction in view of the distances to be bridged, superfluous. The smaller vessels only branch off close to the places where other elements move over relatively small distances. The carotis enters the head region close and caudal to the joint of the lower jaw, where it splits. The next branching lies caudal to the foramen nervi trigemini.

6. *The glands*

An essential component at the swallowing of a big prey is a number of glands, which excrete a product serving for the gliding of the prey and the digesting. Snakes that kill their preys by venom have a glandula venenata.

The functional aspects of a poison-gland concern:

1. production of a minimum amount of venom
2. injection of the venom into the victim within a short time.

The minimum amount required depends on the chemical-physiological property of the poison for the prey. The chemical properties (SLOTTA, 1953) and the lethal dose (HAMILTON FAIRLEY, 1929; KELLAWAY, 1929) of the poison of many snakes is known. A correlation between these properties and those of the gland-cells in respect of their number, size and situation is lacking, however.

The general outer shape of the gland is, concerned to its functional properties, not restricted to any special shape. The position of the gland is, broadly speaking, between the old upper jaw and the neurocranium. A comparison of different venomous snakes learns, that the shape is more or less equal to the room left between upper jaw and neurocranium. Only the genera *Causus* and *Doliophis* show a poison-gland that passes the quadratum (HAAS, 1952).

The position of the gland is correlated with the adductor muscles, in this respect that the gland does not reach more caudally than the adductor muscles and therefore it must be determined more or less by the space left between these muscles and the lip.

This strong connection with the adductor muscular system must be considered an adaptation to the special way of killing the prey. The bite in the poisoning act is mainly caused by the adductor system. The penetrating of the poison-fang into the prey occurs then simultaneously with the injection of the venom. KATHARINER (1900) and HAAS (1931) and many other authors (WOLTER, 1924) following HAGER (1906) meant that the musculus adductor externus superficialis should empty the poison-gland like a hand presses a ball (HAGER called this muscle the musculus compressor glandulae). However, the muscle is not attached over the entire surface of the gland and moreover, the contraction cannot have the character of that of a sphincter, since the fibres run straight to the lower jaw. The gland is pulled ventralwards by the muscle and so a mechanism must be present to resist this movement. Partly this resistance can be given by the liga-

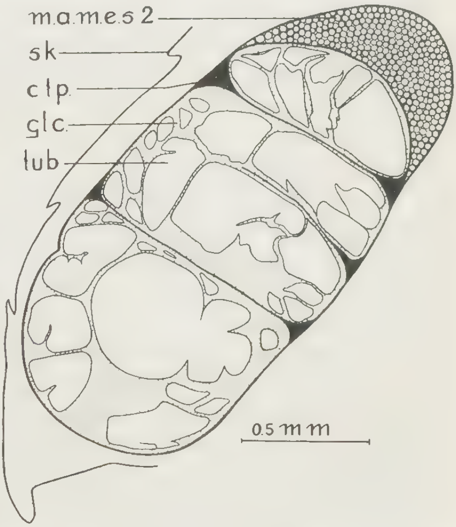


Fig. 46. Transverse section through the left poison-gland from caudal. *c.t.p.*, connective tissue plate; *gl.c.*, gland-cells; *m.a.m.e.s.2*, musculus adductor mandibulae externus superficialis 2; *sk.*, skin; *tub.*, tubular room in the gland.

mentum supratemporale-glandulare, but this is fairly weak and connected to a rather movable bone. The main resistance is caused by the musculus adductor posterior, which pulls the gland dorsalwards.

The demand of a quick excretion combined with a drawing to two opposite sides requires a bottle-like gland. The ductus venenatus and the canales inside the poison-gland lie all in a line. Besides, a special inner structure must be present. The gland will expand into the direction perpendicular on the working-line of the pulling power, or in other words the distance between lateral and medial will be enlarged. If this phenomenon would occur, then no venom could be excreted, especially in the case of a required pressure during the injection. This enlargement now is resisted by some parallel connective tissue plates, running from the lateral to the medial wall of the gland (fig. 46).

The gland is supported by two ligaments, of which the precise function is unknown. They may have a significance in supporting the gland at that stage of the closing of the mouth when the musculi adductores contract. A movement of the gland is prevented then.

The small glands close to the outlet of the duct in the poison-fang excrete, according to WOLTER (1924), a product which closes the canal. The relation between form and function in this gland is unclear.

Concerning the other glands may be stated, that the large amount of glands and their big size is an adaptation to the swallowing of mammals (FONTANA, 1781; TIEDEMANN, 1813; SEIFERT, 1823; PHISALIX, 1922). A simple correlation cannot be supposed, since the glands have also other functions (BROMAN, 1918, a.o.).

Almost every gland is surrounded by tissue of great elasticity, so that a relatively great pressure is exercised on them. An exception is made for the glandula Harderiana and the glandula nasalis. For these very glands BROMAN (1918) gives other functions, *e.g.* in the functioning of the organ of Jacobson.

Many authors mention the fact of dependence of the size of the glandulae labiales to that of the glandula venenata (REICHEL, 1883; PHISALIX, 1922). The glandula venenata should be a part of a labial gland and so it could only develop as a certain kind of gland. It is quite improbable that this glandula tissue would not show any adaptation to the function of the glandula venenata. In some species of the genus *Vipera* proper glandulae labiales should occur not at all (FAHRENHOLZ, 1937, referring to DUVERNOY, MECKEL, MULLER). According to DITMARS (1912) these vipers eat the same kind of food as *Vipera berus*, an inclination, however, occurs for lizard eating.

The shape of the glandula Harderiana is strongly influenced by the eye. Its rostral side is concave and ventral to the eye it is very narrow. It occupies the area between the eye and the transversum.

Generally the glands may be regarded as organs which occupy a determined room, without a special outer shape.

As for a few other glands, not discussed above, we may refer to Fahrenholz (1937).

7. *The tissue in the mouth-cavity and the skin*

Closely correlated with the ability of swallowing a big prey is the flexibility of the tissue in the mouth-cavity and of the skin. In both cases a similar structure exists, namely a widely folded cover. Apparently the folds in the mouth-cavity are placed rather voluntary. In fact, however, the folds lie on places determined by other elements: the lower jaw, the tongue, the upper jaw and the glottis. The opening, through which the prey can be passed, in extended position is about 9 times that of the opening in closed position, so that a mouse, of which the size is about 10 times the volume of the viper's head can be swallowed. The same holds good for the skin. Here the folds are not determined by other elements in the head, but by the scales. The folds lie between the scales. The flexibility increases considerably at an increase of the number of scales. This is probably the significance of two rows of scales between the labiales and the eye, and the division of the parietale and the temporale into a great number of scales. In the area dorsal to the eyes no stretching can occur. Many Viperidae show a large supra-oculare and a large frontale (Schreiber, 1912).

B. THE BRAIN AND THE CEREBRAL SKULL

In a study of the correlation between the functional components and the entire head it would be necessary to divide the brain into parts which belong to the distinct functional components. However, such a consideration is impossible, since the function of many parts of the brain is unknown. Therefore we can only make some rough remarks and consider the entire brain.

More or less belonging to the feeding mechanism the ventral part of the myelencephalon may be regarded as an adaptation to the great extent of the feeding mechanism. The great extension of the myelencephalon and its far ventral position may be understandable in this respect (Ariens Kappers, 1934). In the same way are the big telencephalon, the small dien- and mesencephalon understandable. As to the metencephalon no conclusion can be made as yet. Perhaps the lack of limbs is correlated with it (Ariens Kappers, 1934), although the locomotion is rather complicated in snakes.

Generally the brain of the viper is relatively big (Van der Klaauw, 1948, referring to Dubois), so that it occupies an important part of the total space in the head. The volume for the brain is mainly extended in lateral direction, because the height of the cerebral skull is low, in accordance with the outer shape of the head. This outer shape has some significance in the way of creeping. Besides, the outer shape of the brain is also influenced in some regions. The remaining parts have an independent shape.

In the orbital region a correlation exists between the eye and the brain. As we have explained, it is probable that the breadth of the head in the orbital region is dependent on the olfactorial caudal breadth and on the size and position of the maxillaria. The shape of the brain will be influenced by the eye, if the animal is so small that the eye reaches from the skin to the brain. In bigger animals, where the brain and the eye are relatively small, the components do not reach each other and cannot have any influence on each other. Dependent on this situation we shall find either a tropidobasic or a platybasic structure. Both these structures are therefore independent of the movability of the maxillare.

So we find a tropidobasic structure in *Thamnophis sauritus* (L.), *Tropidonotus natrix* (L.), *Chironius carinatus* (L.), *Dendrelaphis pictus* (Gmel.), and *Leptophis ahaetulla* (L.). Platybasic are *e.g. Eunectus murinus* (L.), *Constrictor constrictor* (L.), *Naja nigricollis* (Reinh.), and many others.

The cerebral capsule joins the brain, except in the occipital region. The wall of the cerebral skull is almost everywhere equally thick. Generally the ventral wall is thicker than the dorsal one. This is correlated with the enormous strains exercised on the ventral wall by the prey. On places where the strain is not exercised directly or perpendicularly on the surface the wall is thinner, as is realized under the occipital muscles (fig. 35).

The ventral wall of the cerebral skull ends rostro-laterally in a crista, to which the membrane of the mouth-cavity is attached (fig. 2). The strong strain exercised by the prey on this membrane makes this comparable with an aponeurosis in a big muscle. The same is the case with this crista, which is in functional sense comparable to the crista of an aponeurosis.

Some regional structures are remarkable. First, the hypophysis is surrounded by bone, which results in a local thickening of the ventral wall. Secondly, the double bony wall around the foramen V may be regarded as a strengthening of the lateral wall (VERSLUYS, 1936). Thirdly, the partly median thickening of the frontale is to be considered as an extra resistance to a shearing strain at a connection of two bones. This phenomenon occurs in a less degree in some other connections, *e.g.* in the otical region.

C. THE EYE AND THE ORBITA

For a discussion of the detailed parts of the eye may be referred to FRANZ (1934) and TRENDELENBURG (1943).

Important in this investigation is the fact that in an optical apparatus with lens structures the retina must have a concave plane. Or in other words, the eye will always be a more or less spherical element (TRENDELENBURG, 1943).

Dependent on the use in dark or in light the eyes of snakes have either a long or a short vestibulum (FRANZ, 1934), which is clearly perceptible in the outer shape. Many authors (BROMAN, 1919; FRANZ, 1934) have emphasized the functional correlation existing between the fixed transparent skin-part over the eye (the so-called fused eyelids), the size and outlet of the glandula Harderiana, the organ of Jacobson and the bifurcated tongue.

The orbita has about the same shape as the eye. The wall joins the eye mainly dorsally and medially. Concerning the correlation between the position of the eye and the brain may be referred to the chapter on the brain. The orbita has a concave shape. At the place where the cerebral capsule joins the orbital wall it has the shape of the orbita (fig. 31). At the place where cerebral capsule and orbital wall diverge dorsally the cerebral capsule is not influenced and between both bony layers is left a shallow groove. The praefrontale is concave where forming the rostral orbital wall. Since the olfactorial capsule also invaginates the praefrontale and the ductus of the glandula Harderiana passes through it, the problem of the conduction of the pressure from the maxillare arises. The resistance to this strain requires a certain size of the surface of the transverse section. The ductus passes the joint with the maxillare laterally, so that no strain can be exercised in this area. This course of the ductus must be regarded as an adaptation to the functions of strain-conduction of the praefrontale, for it runs from the glandula a little laterally, and bends medially rostral to the praefrontale. The main strain is conducted along the medial side, which is the shortest distance between the joint with the maxillare and the roof of the cerebral skull. The thin plate, however, left between the orbita and the olfactorial capsule has hardly any resistance to flexion in a caudal-rostral direction. The lateral plate in the parasagittal plane and lateral to the ductus may be considered an adaptation to such a strain. For the resistance to pressure it plays hardly any rôle, because of its far lateral position. The pressure exercised by the maxillare is mainly attached medially.

The roof of the orbital wall is membranous, and may be considered as a place with no or hardly any resistance to strain. The only strain to occur is via the eye. In extreme circumstances during the swallowing act a small pressure is exercised on the eye. The main part of the strain is resisted by the ligamentum orbitale superior.

The caudo-ventral part of the orbita is not closed and is occupied by some soft parts, joining the eye in form.

D. THE NOSE AND THE ORGAN OF JACOBSON

The nose and the organ of Jacobson are functionally closely related (Broman, 1919; Kahmann, 1932). No data, however, are to our disposal about the relation between the surface of the epithelium and the smell susceptibility, nor about the relation between both organs. The size of the olfactorial capsule differs in different snakes. Generally this capsule is relatively smaller in bigger snakes, as shows a comparison in *Crotalus* and *Lachesis* (*cf.* Versluys, 1936). Since the maxillare in the bigger species is of a rather big size, the capsule is placed there relatively more medial than rostral to the maxillare.

The lateral position of the outer opening of the nose has a biological significance for the creeping way of living and the looking for prey in holes. A general comparison with species which have another way of living shows a relation between the position of the opening and this way of living (Kathariner, 1900).

The position of the nostril determines one end of the olfactorial tunnel. The choane determines the other end. Between both ends the tunnel has a quite different shape in different species.

E. THE OTICAL REGION

The acoustic organ is realized among many other things in the columella auris, which in the viper runs from the quadratum to the fenestra ovalis. No experimental evidence could be obtained on a acoustic susceptibility (Adrian, 1938). The remark of Von Buddenbrock (1952) that the lack of a tympanic membrane should make hearing impossible, need not be right. The connection of the columella with the quadratum and the membranous connection of the stapes in the fenestra ovalis indicates just in the opposite direction. If snakes are deaf indeed, then the presence of a columella is hardly to understand.

The statical organ gives no motive for a discussion.

F. THE TONGUE

For the relation between form and function of the rostral part of the tongue may be referred to Broman (1919). The total length of the tongue is twice as long as the part which must be put out, because the contraction of the muscles is about 50 %. The simple shape of the tongue and tongue-bone is only to understand in negative sense. The simple movement (putting out and retracting and an oval oscillation) requires only a simple structure.

G. THE GLOTTIS

The glottis lies close to the choane, which assures a continuation of the respiration in a closed position of the mouth. The position of the choane has no significance in the swallowing act, as GÖPPERT (1937) states. The glottis is pressed against the tongue during the swallowing act, so that the distance between the choane and the glottis is enlarged. This situation probably takes place in every snake. In one viper, which had swallowed the prey halfway, it could be observed by lifting the prey with a forceps. In pictures of a python the same situation could be observed (pictures of a snake film made by the "Wissenschaftliche Film", Göttingen).

Besides these direct observations this situation could be derived from the position of the muscles which move the glottis. The glottis is closed during the swallowing act and respiration does not occur.

VI. THE NATURE OF THE CONNECTIONS

In the foregoing chapters an explanation was given of the relations and connections of the elements in the head of the viper. The connections of the elements are very close, thus forming the functional components. Considering the entire head no separate and loose functional components can be distinguished as VAN DER KLAAUW (1945) could assume at the outset of his conception in relation to the skull. The close connection includes a considerable influence of the elements on each other. This influence is of different character: structural, positional or functional. Moreover, the structure, shape and position of an element depends on the function required in the mechanism (fig. 38). The number of factors influencing an element is relatively small. The elements have a rather high degree of individuality; they are arranged in a pattern, in such a way that the correlation is mostly indirect (table II).

In principle it is possible to divide the head into a number of functional components. However, this division will be artificial, because of the connection and the dependence of the elements of different functional components.

In spite of this imperfection in the division, the functional components can be distinguished even on different levels. In general these components are built of different tissues, only on a quite low level the component may be formed by one tissue. Therefore the distinction of these tissues will not coincide on the whole with the division of functional components.

A division of these functional components into smaller functional units: apparatus, constructions, constructive elements *etc.*, leads to the distinction of different parts as functional elements in these components on a higher level. The components are built of different elements, which may have different properties concerning their composition of tissues, *e.g.* a component may have a skeletal part, a musculous part, a nervous part, *etc.* If these smaller parts are connected now by that part of a construction which has equal properties, then a connection of these elements to a unity is possible, *e.g.* the cerebral skull, the old upper jaw, the lower jaw. These unities are morphological unities as distinguished in the systematic anatomy but are not equivalent to functional unities. Consequently the skull or the muscular system cannot be considered as a functional unity. A division of functional components for these parts seems therefore less valuable.

TABLE II

	glottis	choane	tongue	nose	org. Jac.	glands	tiss. i. m	vomer	praefr.	eye	m. protr	m retr	cerv m	cerebrsk	maxill.	transv	pterys	teeth	m. angle	pois gl	pois f.	brain	cansem.	suprat.	quadr.	m. add.	m. add. pl	m. depr.	low. jaw
glottis		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
choane	p		s	s	—	—	—	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
tongue	—	s		—	—	pr	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
nose	—	p	—		s,p	p		—	s		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
org Jac.	—	s	pr	s,p		pr	—	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
glands	—	—	—	—	—		—	—	s	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s	—	—	—
tiss. i. m	—	—	—	—	—	—		—	—	—	—	—	—	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
vomer	—	—	—	—	—	—	—		—	—	—	ps	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
praefr.	—	—	—	—	—	—	—	—		—	—	—	—	s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
eye	—	—	—	—	—	—	—	—	s		p	p	—	s	p	p	—	—	—	—	—	—	—	—	—	—	—	—	—
m. protr.	—	—	—	—	—		—	—	—	—		—	—	s	s	s	s	—	—	—	—	—	—	—	—	—	—	—	—
m. retr	—	—	—	—	—	—	—	s	—	—	—		—	s	pr	—	s	—	—	—	—	—	—	—	—	—	—	—	—
cerv. m.	—	—	—	—	—	—	—	—	—	—	—	—		s	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
cerebr. sk	—	—	—	—	—	—	—	—	—	—	p	p	p		—	—	—	—	—	—	—	s	p	p	—	p	—	p	—
maxill.	—	—	—	—	—	—	—	—	s	—	—	—	—	—		s	—	—	—	—	p	—	—	—	—	—	—	—	—
transv.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s		s	—	—	—	—	—	—	—	—	—	p	—	—
pterys.	—	—	—	—	—	—	—	—	—	—	p	p	—	—	—	s		p	—	—	—	—	—	—	p,s	—	p	—	—
teeth	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s		—	—	—	—	—	—	—	—	—	—	s
m angle	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—	—	p	p	—	—
pois. gl.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		pr	—	—	—	p	—	—	—	—
pois. f.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s	s	—	—	—	pr		—	—	—	—	—	pr	—	—
brain	—	—	—	—	—	—	—	—	—	—	—	—	—	s	—	—	—	—	—	—	—		p	—	—	—	—	—	—
cansem	—	—	—	—	—		—		—	—	—	—	—	s	—	—	—	—	—	—	—	s		p	—	—	—	—	—
suprat.	—	—	—	—	—	—	—	—		—	—	—	—	—	—	—	—	—	—	—	—	—	—		s	—	—	—	—
quadr.		—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s	—	—	—	—	—	—	s		p	—	p	s,p
m. add.	—	—				—	—	—	—	—	—	—	—	s	—	—	—	—	—	s	—	—	—	—	s		—	—	s
m add pl	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s	s	—	—	—	—	—	—	—	—	—		—	s
m. depr.	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	s	—	—		s
low. jaw	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	p	—	—	—	—	—	—	s	p	p	p	

The influence of some elements on each other. On the short side are placed the influencing elements, on the long side the influenced elements. *p*, positional; *pr*, by presence; *s*, structural. Further explanation in the text.

The distinction of components on different levels leads to a hierarchical system of which the realizations of the so-called main functions (fig. 38) form the toplevel. The lowest level which can be seen lies in the microscopical field or still farther.

On every level now the problem arises of how the components are related to their function, how they depend on each other, how they are connected and how their form is totalized. Many of these dependences, connections and integrations are elucidated in the preceding chapters.

The most remarkable fact in the integrations of the lower functional components into a higher one is that they are connected by parts of them, so that in most cases the other parts of the components do not show a direct correlation, but an indirect one. They form a pattern. The appearance of this pattern not only depends on the connection of the components by means of their parts, but in addition it also depends on the size and the outer shape of the animal and the relative size of the prey.

By these indirect and complicated influences the determination of indices of rather at random chosen elements is rather disputable. Generally the indices show a different trend, in only few cases do the relations indicate in similar directions (KLAUBER, 1939; ANTHONY, 1955). Nevertheless the differences in trend may show a similar tendency in the pattern. It seems more valuable to start at first with a research into the significance and the relation of the elements in the pattern.

The so-called "untransparent" relations (VAN DER KLAAUW, 1950) can be understood in the same way.

It may be remarked that a real comparative functional morphology is based on a comparison of the patterns of different taxa.

The connection of the components is quite different in many cases, hence many problems may arise. The only problem mentioned here occurs if one element has several functions. In this case four possibilities exist:

1. a realization of every function in this element separately
2. a structural compromise
3. a total shape being an integration in that every component is entirely realized, but the shape is unequal when the components are simply added
4. or a structure, which allows more functions for the same element.

A realization of every function separately is found in the pterygoid, concerning the placing of the teeth and the mechanical resistance to muscular tension; in the shape of the pterygoid concerning the places of attachment of the musculus adductor mandibulae internus pterygoideus accessorius and the musculus protractor pterygoidei; in the maxillare concerning the dorsal ridge of the joint with the transversum and the maxillare itself; the presence of cristae on the parietale, occipitale and other elements and the bony elements themselves.

Some examples of a structural compromise are: the courses of the musculus levator and the musculus protractor pterygoidei; the joint between the transversum and the pterygoid; the course of the ductus Harderianus; the relatively fixed position of the eye, *etc.*

Examples of an integrated structure are: the maxillare, the transversum, the middle part of the pterygoid, the part of the lower jaw rostral to the joint, the musculus retractor vomeris. The integration lies frequently on a microscopical level.

A realization of every function separately requires in many cases also a microscopical integration.

A structure that serves for more functions is found in bones, which have a resistance to different strains. These strains must have then an equal influence, *e.g.* the size of the surface of a transverse section can be the same in resisting a pressure or a transverse strain of equal amount.

Another example of this situation lies on a higher level. The upper jaw serves for the swallowing and the injection acts. The cervical muscles function in the movement of the head during the swallowing act and the locomotion and injection. In these cases the function of the small elements is the same, whereas the coordination of the smaller components differs.

Besides these connections of the functional components of the constructions or of parts of them, the connection of the tissues in these parts is of interest.

The way of attachment of the muscles to the bone is to depend on the structure of the muscle (DULLEMEIJER, 1951, 1952; ROOTH, 1953; VAN VENDELOO, 1953).

In the viper many muscles are simple ones (DULLEMEIJER, 1952), in some cases a surface aponeurosis exists. The muscles with an aponeurosis are attached in two ways:

1. the aponeurosis is attached to a crista, *e.g.* the cervical muscles and the musculus pseudotemporalis

2. the aponeurosis is tangentially attached to a flat surface of an element, *e.g.* the musculi adductores externi.

In one case the aponeurosis is narrow and thus the crista is small, having the appearance of a spina, *e.g.* the spina on the basisphenoid (*sp.b.sph.*). In three other cases a tendon is attached to a spina, *e.g.* the musculus retractor vomeris, the musculus retractor quadrati and the musculus adductor pterygoidei.

The way of attachment is important in relation to the function of the muscle in the whole pattern, as has been discussed in the preceding chapter.

Musculous attachments are sometimes placed on surfaces with a slight excavation, *e.g.* the musculus depressor, some cervical muscles and the musculi protractores.

A reversed correlation between cristae and aponeuroses does not occur. Many aponeuroses are attached to a crista, but every crista does not bear an aponeurosis. First, other connective tissue elements may be correlated with cristae, *e.g.* the attachment of many ligaments, the attachment of the tissue in the roof of the mouth. Secondly, cristae may occur which can be regarded as freely projecting margins of a plate-shaped extension serving as mechanical resistances, *e.g.* the wing of the pterygoid and the extension of the lower jaw rostral to the joint.

The connections of ligaments and bones equal those of aponeuroses and bones.

A direct connection between nerves and bloodvessels and the bone does not exist, although an influence of these elements on the bone may be mentioned.

With a distinction of functional components on different levels no objections can be made calling the foramina, places for the passing of nerves and vessels, functional components. These components may be considered as lying on the same level as the components serving for the attachement of muscles.

VII. SUMMARY

In this study a morphological description of the elements of the head of the common viper, *Vipera berus* (L.), was given.

Starting from the conception whereby the head is considered a totality built of several functional components, the relation of these components to each other has been discussed.

It has been shown that these functional components are related in such a way that a pattern is formed.

The functional components are considered as structural realizations of the functions.

The realization of a functional component is dependent on the material of which it has been built, on the requirement of the function, on the relation to other functional components and on the rules consisting between the form and the function in the realization.

It could be demonstrated that there are four possibilities of influences for the relation of the functional components to each other.

1. The realization of a function into a structure is separate for every function. The realizations can be added, so that an additional structure is formed.

2. The realization for several functions is quite the same, so that the same structure has several functions.

3. The realization is an integrated structure.

The shape of this structure is unequal to the structural realization of every separate function; it has, however, the significance of a complete realization of the function.

4. The realization is a compromise. The shape of this structure favours the functions incompletely.

The nature of the connections in the pattern is rather loose, so a high degree of individuality of the elements exists.

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THE DEVELOPMENT AND COORDINATION OF LARVAL LIMB MOVEMENTS IN TRITURUS TAENIATUS AND AMBYSTOMA MEXICANUM

(WITH SOME NOTES ON ADULT LOCOMOTION IN TRITURUS)

by

J. FABER

(*Laboratory for Comparative Physiology of the State University of Utrecht, and Hubrecht Laboratory, International Embryological Institute, Utrecht*)

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I. INTRODUCTION

The present investigation was started with the aim of testing the applicability of Coghill's well-known results, obtained in *Ambystoma punctatum* (1929), to other Urodele species. In the course of the work so many differences between *Ambystoma punctatum* and the two other species investigated became apparent, that a rather detailed description of the larval limb movements in these two species seemed justified. This description may be of value both from a comparative physiological point of view, and as an extension of the basis needed for further experimental analysis of the locomotion pattern in Urodeles.

In the light of the new facts, which concern both the first origin and the later coordination of the limb movements, COGHILL's findings will be discussed.

In connection with the study of the development of coordination of the limb movements interest arose in the external (environmental) factors determining the nature of the locomotion pattern as a whole. The tentative experiments on adult animals reported in the second part may be regarded as supplementary to the important work carried out by GRAY and others with regard to the internal (organismic) factors acting in the Amphibian locomotion pattern.

II. METHODS

The mobility of the larval limb buds and limbs was tested in different ways. First of all mechanical stimulation was applied by means of a human hair mounted in a glass tube. Besides this the postural movements were tested, either by tilting the animals in different angles and around different axes by placing them in different positions against the sloping walls of the embryo dishes in use, or by using a simple, hand-moved horizontal turning table. The latter was provided with a paper collar, so as to exclude optic stimulation in the horizontal plane. Optomotor reactions associated with the perception of objects above the turning table may have played a role.

Other methods will be discussed in the course of the paper.

III. STAGING

For reasons of easy comparison a uniform set of stages has been defined, comprising all three species, and based only on limb development, as set apart from overall bodily development, which shows considerable differences in the three species. It has been attempted to remain as close as possible to both GLAESNER's Normal Table for *Molge vulgaris* (*Triturus taeniatus*) (1925) and HARRISON's unpublished Normal Table for *Ambystoma punctatum*. The following table gives the relationships between the three sets of stages, as well as a short description for each stage.

Stage	Description	Glaesner St.	Harrison St.
	Fore limbs		
I	Two fingers indicated	38	41
II	Fingers distinct	39	42
III	Fingers larger	40	43
IV	Third finger indicated	—	44
V	Third finger distinct, elbow still straight, hand still vertical	41	—
VI	Elbow bent slightly, hand pronated about 45°	—	45
VII	Hand horizontal, resting forearm transverse	—	46
VIII	Resting forearm obliquely or straight forward	42	—
IX	Fourth finger indicated	43	—
	Hind limbs		
X	Two toes indicated	—	—
XI	Toes larger	48	—
XII	Third toe indicated	—	—
XIII	Third toe larger	49	—
XIV	Fourth toe distinct	—	—

IV. COGHILL'S FINDINGS IN AMBYSTOMA PUNCTATUM LARVAE

In a widely known little book Coghill (1929) described the origin of the locomotion pattern in *Ambystoma punctatum.* This work having been used by many authors as a basis for further research (also in non-Amphibians), as well as for theoretical considerations and even for speculations (cf. Hooker, 1952), the question arises whether such an extensive generalization of his findings is admissible. Before trying to give an answer to this question, a short account of Coghill's main results must be given here. In reading this, it must be borne in mind that the stage numbers used have only approximative value, as the stages had to be estimated after descriptions and figures in Coghill's book.

As in other Urodeles, in *Ambystoma punctatum* the fore limbs develop much in advance of the hind limbs. The first fore limb movement (stage I) consists of adduction and abduction. This movement at first occurs only as an integral part of the action of the trunk musculature, and only later (stage VI to VII) an independent local reflex arises from the initial "total pattern" by a process of "individuation". The first limb movements to become more or less independent are the postural reflexes. Moreover the exteroceptive reflex mechanism is at first sensitized by a postural response acting at the same time.

The hind limb movements also show "individuation" out of an initial "total pattern". The first integrated movements appear about stage XII, the first autonomous movements about stage XIV.

In the development of coordinated locomotor movements of the limbs the initial phases also show a total integration of trunk and limbs. The first spontaneous locomotor movements of the fore limbs consist of simultaneous protraction and retraction (stage VI). The first actual walking movements (stage VII) are accompanied by lateral flexure of the anterior part of the trunk, in such a way that the convex side is the side where the limb is protracted, whereas the limb on the opposite side is retracted (see Fig. 1 B). Only in a much later stage the limbs are capable of autonomous alternating movements without trunk movement.

The initial walking movements of the hind limbs (stage XIV) are also integrated with trunk movements, but in the opposite way (retraction at the convex side, protraction at the concave side) (see Fig. 1 B). The hind limb movements lag behind the fore limb movements with an interval equal to the time needed for the trunk flexure to pass from the pectoral region to the pelvic region. COGHILL's conclusion is that initially the swimming movement of the trunk is the dominant factor in walking, and that only later this factor is gradually replaced by a pattern of coordination between more or less independent limb movements.

In the following we will find opportunity to point out essential similarities as well as essential differences between the pattern as described by COGHILL and the pattern found in the two other Urodele species.

V. INVESTIGATIONS IN TRITURUS TAENIATUS LARVAE

It was attempted to determine exactly the stage at which the first fore limb movements occur in *Triturus*. This was found to be stage III. In stage I and II the limbs could never be brought to a response of any kind. The first movements in stage III are already of two different kinds. First of all, on tilting the animal around the longitudinal axis, a weak postural reflex becomes evident in the form of a slight elevation of the upper limb, sometimes accompanied by slight abduction and some supination. The limb is kept in this position as long as the tilt continues.

In the second place mechanical stimulation may, although very seldom, evoke a response, the nature of which it is difficult to determine. Since mechanical stimulation of these small limbs naturally involves a good deal of passive movement of the limb, the response may in fact be of one of the following types: true tactile reflex, "stretch" reflex, or "myogenic "movement. A response usually occurs only after repeated stimulation of the upper surface of the hand, and only when stimulation has not gone on for too long. The responses consist either of a swift and short elevation and abduction, followed by a return to the original position (a movement comparable to the postural reflex described above) or, very seldom, of a short and swift adduction-abduction movement accompanied by slight elevation (a movement comparable to the first fore limb movements in *Ambystoma punctatum*).

If these responses should be of true reflexogenic nature, it is important to note that from the very first beginning they occur without any indication of accompanying action of the trunk musculature: the first fore limb movements seem to be entirely autonomous, and apparently are not integrated in a "total pattern".

In stage IV the postural reflexes occurring on lateral tilting include also a movement of the lower limb, which is depressed as long as the tilt continues. A tilt around a transverse axis now results for the first time in adduction of both limbs, if the head is lifted, and abduction if the head is lowered.

In stage V the limbs for the first time show a response if the animal is placed on the turning table and turned very slowly. As already mentioned, this may be either a postural response, or an optomotor reaction. Simultaneously with, or a short time after lateral flexure of the head against the direction of turning, now the limb on the convex side is adducted slightly, whereas the opposite limb shows distinct abduction with slight supination and very slight flexion. This pattern of movements, which later will play an important role in the first spontaneous limb movements, will henceforth be referred to as the "basic pattern" (see Fig. 1 C). It should be noted that the pattern is opposite to the pattern of initial spontaneous locomotion in *Ambystoma punctatum* and to the locomotion pattern of adult Urodeles, which patterns are characterized by abduction (protraction) of the limb on the convex side, and conversely. On the other hand the pattern is principally identical with the pattern exhibited on the turning table by adult Urodeles, either as a postural or as an optomotor response.

In stage VI the basic pattern occurring on the turning table is more differentiated, the limb on the convex side showing not only adduction, but extension as well. Sometimes during prolonged turning this adducted and extended limb may make one single distinct stepping movement, consisting of swift protraction with slight flexion, followed by slow return to the adducted position.

At the same time the first spontaneous coordinated limb movements

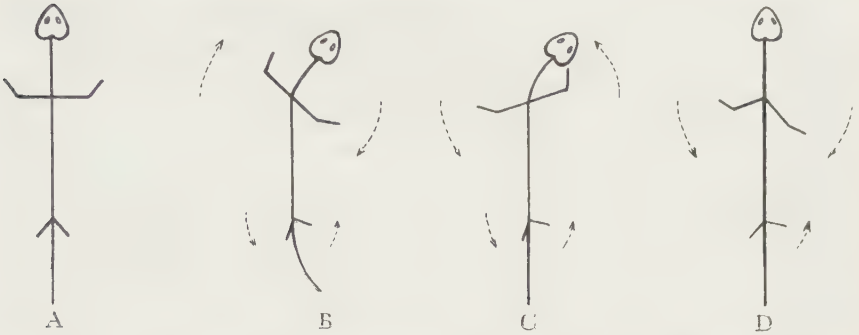


Fig. 1. Diagram illustrating different patterns of spontaneous limb movements in Urodele larvae. A. Resting Urodele larva. B. Initial walking with all four limbs in *Ambystoma punctatum* (according to Coghill, 1929). C. "Basic pattern" in *Triturus*, preceding actual walking. D. Initial walking with all four limbs in *Triturus* ("parallel coordination").

occur, and from the beginning these take the form of the "basic pattern", which means that their coordination with the head and trunk movements is opposite to that observed in the early movements of this kind in *Ambystoma punctatum.* Usually, but not always, the movements are induced by the perception of a moving object ("prey"). We may call this type of movements "pre-ambulatory locomotor movements", since they may bring about some motion of the body as a whole without as yet being true walking movements.

The same "basic pattern" is now also performed as a postural response to lateral tilting, that is to say in combination with the already existing postural reflexes: the head is bent towards the upper side, the upper limb is elevated, protracted and slightly flexed, whereas the lower limb is depressed, adducted and extended. The entire pattern is most pronounced if the animal is placed against the sloping wall of the dish with its head pointing obliquely downwards. In this position it frequently happens that the lower limb (the limb on the convex side) makes one or more successive stepping movements.

In this stage the limbs become also involved for the first time in the "catching movement". This quick forward jumping movement of the whole animal, already established in the previous stage, is now frequently introduced by simultaneous retraction of both limbs, and this retraction movement may also occur by itself as a reaction to moving objects. Simultaneous protraction may also occur, as in *Ambystoma punctatum*, but this may well be of a postural nature, as it is seen only during or shortly after the "catching movement", not before it.

As regards the responses to mechanical stimulation, among which up till now the quick elevation movement predominated, we see how in this stage a new slow adduction response makes its appearance.

In stage VII there appear for the first time unilateral and autonomous spontaneous limb movements, which are, as far as could be ascertained, confined to either elevation or adduction-extension movements. The responses to mechanical stimulation have become of a much more differentiated nature. The predominating response now is adduction, accompanied by either pronation, elevation or total extension. On prolonged stimulation a totally adducted limb may now perform movements which may be regarded as introductory to a true "stepping reflex". Sometimes a hardly perceptible, very short and quick flexion movement of the elbow occurs, but in other instances already a protraction of the entire limb is observed, in which case the elbow hardly flexes. Also independent reflectory movements of the wrist occur.

It must be mentioned here that sensitizing of reflexes by postural responses, as observed by COGHILL in *Ambystoma punctatum*, has not been seen in *Triturus* (nor, for that matter, in *Ambystoma mexicanum*).

In stage VIII short and weak responses and independent responses of parts of the limb have been replaced to a considerable extent by complete, well integrated and stereotyped stepping movements. The complete stepping movement consists of flexion of the elbow, immediately followed by protraction of the entire limb and subsequent simultaneous retraction and extension. In later stages the limb responses become again less stereotyped, and the frequency of responses of parts of the limb increases once more.

A new type of response is established in stage VIII: the withdrawal-reflex. It occurs on strong stimulation and consists of retraction, or adduction with flexion.

Alternating walking movements of the fore limbs have not appeared even now. Only several days later they occur for the first time, viz. in stage IX, that is at a relatively much older stage than the stage at which *Ambystoma punctatum* exhibits its first walking movements. In *Triturus* the walking movements are from their first appearance independent of any action of the trunk musculature, in contrast to the "basic pattern" movements of previous stages. The "basic pattern" as a spontaneous activity is gradually replaced entirely by the autonomous walking movements, although it remains functional as a postural response.

Simultaneous protraction and retraction of the fore limbs occurs very seldom now. Usually one of the limbs is ahead of the other. As a rule retraction of the fore limb proceeds more slowly than protraction, so that the retraction phase lasts longer than the protraction phase.

The walking movements may be represented tentatively in the following diagram, which should be read from left to right:

Left ——— = ——— = ———= — retraction
Right =——— = ——— = ——— = protraction

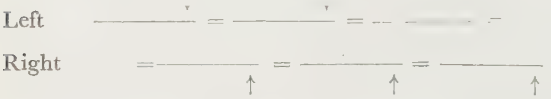
We now proceed to the description of the movements of the hind limbs. The next stage, stage X, is much older than stage IX, in which the hind limbs are not yet even visible. In stage X and XI no responses could be evoked in the hind limbs by mechanical stimulation, except very weak, twitch-like movements of a questionable nature in the hip and knee joints.

In stage XII already two kinds of responses have been established, viz. distinct elevation-adduction or, more seldom, distinct abduction. The movements may be accompanied by flexure of the trunk, but it has been definitely ascertained that from their first origin they can occur also independent of movements of the trunk (or of the fore limbs, for that matter). However, they apparently show a stronger coordination with trunk movements than do the fore limbs.

Spontaneous movements also appear already in this stage, but these are never entirely independent yet. They are restricted to abduction, as yet usually unilateral, and they occur either together with concave flexure of the trunk, or in coordination with fore limb movements. The nature of this latter, initial coordination is as follows: the movement as a rule occurs during retraction of the fore limbs, at that side at which fore limb retraction is most advanced, and at the moment at which the retraction phase of the ipsilateral fore limb in question is nearly completed. Protraction of the contralateral fore limb is not a necessary condition. In other words, this initial coordination seems to be primarily a coordination between ipsilateral limbs, in short a "parallel coordination" instead of the "diagonal coordination" which is known from the adult Amphibian, and particularly the Anuran locomotion pattern (see Fig. 1 D). However, other combinations of limb movements have been occasionally observed, which did not follow the rule of parallel coordination, and which indicate that a relative independence between the limb movements exists already at this early stage. A further general observation is the fact that spontaneous movements of the hind limbs occur very seldom without simultaneous or immediately preceding movements of the fore limbs. This applies also to older stages.

In stage XIII entirely autonomous spontaneous abduction movements of one hind limb have been observed. In this stage the hind limbs begin to take part in the "basic pattern", either in the form of a spontaneous movement or as a postural reflex. The hind limbs move in the same sense as the fore limbs, i.e. abduction on the concave side and adduction on the convex side. (See Fig. 1 C). Ipsilateral limbs consequently move in the same sense in the basic pattern, in contrast to the opposed movement of ipsilateral limbs in locomotion. The hind limbs exhibit the "basic pattern" movements only if head or trunk flexure (not necessarily in the sacral region) takes place at the same time, in contrast to the fore limbs, which in these later stages may perform the "basic pattern" without participation of the head and trunk.

In the meantime the "parallel coordination" has developed in such a way that a diagonal pattern of limb movements results, which resembles already the adult locomotion pattern. It may be represented tentatively by the following diagram:



— fore limb retraction
= fore limb protraction
↓↑ hind limb protraction

We see from the diagram that protraction of the hind limbs usually occurs shortly after protraction of the contralateral fore limb. Therefore the possibility must be taken into account that besides "parallel coordination" also a certain degree of "diagonal coordination" may be operative in the present pattern. The question whether and to what extent this is the case, and which relative parts the two coordination mechanisms play in the later locomotion pattern, can only be answered by appropriate experiments. At any rate it is a fact that in normal circumstances also when the ipsilateral fore limb does not move, protraction of a hind limb usually occurs after or simultaneously with, and only very seldom before protraction of the contralateral fore limb, so that we must conclude to the existence of a definite diagonal interdependence between the movements of contralateral limbs.

In the hope of acquiring some further insight in the later development of coordination, some amputation experiments have been performed on older larvae. Amputation of one or both hind limbs has no perceptible effect on the movements of the remaining limbs. On the other hand, amputation of a fore limb has an obvious effect on the type of movement and the posture of the ipsilateral hind limb. The resting hind limb on the amputated side shows an almost permanent stronger adduction than the other hind limb, and often also a stronger flexion of the knee and the fingers. Moreover the limb is often characterized by exaggerated flexion during protraction. All this may point to a decrease in tonus or a partial paralysis of the abductors and extensors of the hind limb, owing to amputation of the ipsilateral fore limb. These results support the notion of a "parallel coordination" between the larval limbs. It must be added here that in the adult animal amputation of a fore limb has no effects.

The actual coordination pattern between the limb movements is not altered by unilateral fore limb amputation, notwithstanding the different behaviour of the ipsilateral hind limb. On amputation of both fore limbs, however, it often undergoes a change. This applies also to adult animals. As already mentioned above, in the normal animal movements of the hind limbs very seldom occur without simultaneous or immediately preceding movements of the fore limbs, and particularly protraction of a hind limb hardly ever occurs before protraction of the contralateral fore limb. Now, after bilateral fore limb amputation both phenomena are repeatedly observed, even during several successive diagonal pattern cycles, so that the following pattern may be seen: 1. left hind limb - 2.right fore limb stump - 3.right hind limb - 4.left fore limb stump. This means an "inversion" of the normal pattern, which is: 1.left fore limb - 2.right hind limb - 3.right fore limb - 4.left hind limb. It is interesting to note that this inversion can be abolished by narcosis, so that it is apparently of a voluntary rather than of an involuntary nature. In this connection the reader is referred to page 514.

VI. INVESTIGATIONS IN AMBYSTOMA MEXICANUM LARVAE

The Axolotl is distinguished by a relatively much later limb development as compared with the two other species, in which limb development occurs at comparable stages of bodily development. On the other hand, in both *Ambystoma* species function starts in earlier stages of limb development than it does in *Triturus.*

The very first responses of the fore limbs to mechanical stimulation occur in stage I. In nearly all cases these responses are accompanied by adduction movements of the ipsilateral gills or of the gills of both sides, or at least by twitches of the gill musculature. Moreover, there exists a rather strong correlation between both fore limbs, as often a unilateral response is followed after a short time by a similar movement of the other limb. Nevertheless in a few instances responses not accompanied by any visible action of trunk, head or gill musculature have been observed. These are, in other words, completely autonomous responses.

The responses are of two different kinds. First of all a weak abduction movement may occur, accompanied either by supination or by elevation. This response may perhaps be regarded as introductory to the second type of response, which might be called a "rotation" movement. In this movement the tip of the limb describes an ellipsoid. The movement is a combination of abduction-adduction, elevation-depression and supination-pronation. It may be regarded as a very early differentiated, primitive stepping movement.

Postural responses on lateral tilting do not occur before stage III. In that stage slight elevation of the upper limb and distinct depression of the lower limb are observed, and the lower limb sometimes makes an incomplete protraction movement without flexion, i.e. an incomplete stepping movement. The same movement may now occur as a tactile reflex. Recognizable limb responses on the turning table do not occur before stage VII, which is very late in comparison with *Triturus*.

Spontaneous limb movements of several kinds also make their appearance in stage III. First of all one observes simultaneous retraction-protraction movements as a response to moving objects ("catching movement"). Spontaneous unilateral adduction has also been observed. Finally spontaneous, unilateral, incomplete stepping movements are sometimes performed. These always occur in combination with spontaneous lateral flexure of the head away from the stepping limb, while the other limb is sometimes protracted without stepping. The latter particular indicates that we have to do with a pattern similar to the "basic pattern" performed by *Triturus*, but in an advanced stage. But for the absence of initial adduction and extension of the limb on the convex side the pattern is essentially the same as that exhibited by *Triturus* in stage VI, during prolonged turning on the turning table (see page 502).

In stage IV the complete stepping movement has been established, which is characterized by complete protraction in combination with elevation-depression, the tip of the limb describing a curved line. The elbow is not yet flexed. The stepping movement performed as a tactile reflex is sometimes preceded immediately by a short adduction movement. This is of interest because it suggests a parallel with the adduction response frequently occurring in stage VI and VII of *Triturus* (see page 504). Apparently here, as in the "basic pattern" described above, the introductory adduction movement is either altogether missing, or considerably shortened as compared with the responses in *Triturus*.

Flexion of the elbow during stepping occurs in stage VI. The most important feature of this stage is the appearance of the first spontaneous alternating walking movements. These movements are in themselves completely autonomous, but there exists a certain parallel with *Ambystoma punctatum* in so far as, if head and trunk happen to be bent laterally previous to locomotion, it is always the limb on the convex side of the body which starts moving. This is, however, never accompanied by adduction of the limb on the concave side, as it is in *Ambystoma punctatum*.

A "basic pattern" entirely comparable to that observed in *Triturus* is established in stage VII as a response exhibited on the turning table. Adduction and extension of the limb on the convex side are accompanied by slight abduction and flexion of the other limb. Sometimes the movements may occur without flexure of head or trunk. The pattern also occurs as a postural response to lateral tilting.

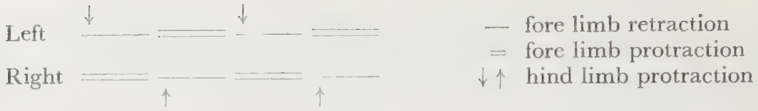
Usually, however, unlike in *Triturus* the limbs react to turning by performing a series of alternating stepping movements, which is here also initiated by the limb on the convex side.

From stage VII onwards no essentially new features appear, so that we may now turn our attention to the hind limbs. In stage X hind limb responses to mechanical stimulation occur for the first time, but only very seldom. The responses are restricted to abduction. Adduction and elevation only appear in a later stage. As far as could be observed the responses are autonomous.

In stage XI only weak responses to equally weak stimuli appear to be entirely autonomous. The stronger responses are always accompanied by concave flexure of the sacral region of the trunk. Apparently, just as in *Triturus*, the hind limb movements are right from the beginning coordinated more strongly with trunk movements than are the fore limbs. Moreover, hind limb movements are usually accompanied by movements of the gills, and often by movements of the fore limbs. Here again we notice the rather strong functional correlation of all extremities characteristic for *Ambystoma mexicanum*.

In stage XI also an adduction response appears. It is usually accompanied by convex trunk flexure, and sometimes by abduction of the contralateral hind limb.

Spontaneous hind limb abduction also appears in this stage. Here again hind limb movement hardly ever occurs without simultaneous retraction of the ipsilateral fore limb, whereas protraction of the contralateral fore limb is not a necessary condition. We have, therefore, again to do with "parallel coordination" of the larval limb movements. The primitive coordination pattern as a whole, however, differs in some respects from that exhibited by *Triturus*. First of all hind limb abduction occurs in the beginning, instead of towards the end of the retraction phase of the ipsilateral fore limb. Secondly the retraction and protraction phases of the fore limbs are equal in duration and do not overlap each other. The following tentative diagram illustrates the pattern:



Here again the pattern does not exclude the possibility of diagonal coordination acting simultaneously with parallel coordination. That this actually is the case in later stages is proved by an experiment performed on a larva of stage XIII, which was in a state of deep chloralose narcosis. Chloralose is claimed to put out of action selectively the higher nervous centres. The larva concerned had indeed lost all spontaneous mobility, but had retained its normal reflex sensibility. When a retraction reflex was evoked in a fore limb, sometimes simultaneous protraction of the ipsilateral hind limb was observed. When a fore limb was induced to protract, however, in several cases the contralateral hind limb made a protraction movement. Here apparently both types of coordination are acting in one and the same stage.

From stage XII onwards the adduction response, with or without elevation, gradually takes the place of the abduction response.

Fore limb amputation in *Ambystoma mexicanum* has effects similar to those described in *Triturus*.

VII. COMPARISON OF THE ORIGIN OF LARVAL LIMB MOVEMENTS IN THE DIFFERENT SPECIES

In order to facilitate comparison the principal results with regard to non-postural movements are summarized in Table I. It should be stressed once more that the stage numbers mentioned for *Ambystoma punctatum* have only approximative value. It would be of interest to repeat the observations on this form, using the staging introduced in this paper.

TAB

Comparison of the time of origin and the type of non-postural limb movements in t bodily development. For d

	fore limb responses		fore limbs, spontaneous, simultaneous	fore limbs, "basic pattern," spontaneous
	only integr. with trunk	autonomous		
Amb. punct. (Coghill)	I, add.-abd.	VI–VII	VI	—
Amb. mex.	—	I, abd.-elev. (sup.), "rotation"	III	III
Trit. taen.	—	III, abd.-elev., add.-elev.	VI	VI

What do these results say with regard to the question whether a generalization of COGHILL's findings is admissible? We think the answer must be in the negative. Both in as closely related a form as *Ambystoma mexicanum* and in *Triturus taeniatus* considerable deviations have been recorded.

Let us first consider the often expressed hypothesis that in general in Vertebrate ontogenesis local reflexes should arise from an initial "total pattern" by a process of "individuation". It has become clear that this hypothesis does not hold for the Axolotl, nor for *Triturus*[1]. In the Axolotl, with its relatively very late, and therefore probably functionally accelerated limb development, it would be possible to think that the individuation process should have been "telescoped" together as compared with *Ambystoma punctatum*, and thus shortened to such an extent as to become altogether latent. In *Triturus* this is already much less probable. There the fore limbs also show, it is true, a retardation in beginning of function as compared with *Ambystoma punctatum*, but the hind limbs become functional at probably about the same stage of overall bodily development. Nevertheless their function can be altogether non-integrated from the beginning.

That in the Axolotl the late morphological limb development has actually resulted in an acceleration of the functional development is suggested by the fact that all non-postural limb functions except the first fore limb responses appear in an earlier morphological stage of development than they do in both other species, and also by the particularly early and rapid development of the stepping movement of the fore limb.

A second important deviation from the pattern described by COGHILL is found in the development of the spontaneous alternating limb move-

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[1] It must be mentioned here that YOUNGSTROM (1938) has also observed autonomous early limb movements in the Anuran form *Pseudacris*.

I

three Urodele species. The staging used is based only on limb development, not on overall finition of stages see page 500.

fore limbs, spontaneous, alternating		hind limb responses		hind limbs, spontaneous, alternating	
only integr. with trunk	autonomous	only integr. with trunk	autonomous	only integr. with trunk	auton., coord. with fore limbs
VII	much later	XII, add.-abd.	XIV	XIV	much later
—	VI	—	X, abd.	—	XI
—	IX	—	XII, add.-elev., abd.	—	XII

ments. The spontaneous "basic pattern" preceding the appearance of the first actual walking movements of the fore limbs in the Axolotl and in *Triturus* is a phenomenon apparently completely absent in *Ambystoma punctatum*[1]. The walking movements themselves, on the other hand, are completely autonomous and do not show the strict coordination with trunk movements which is typical in *Ambystoma punctatum*. The same holds for the walking movements of the hind limbs, so that we must conclude that Coghill's statement, saying that in *Ambystoma punctatum* initially the swimming movement of the trunk is the dominant and coordinating factor in walking, is not valid for the two other species. For the fore limbs "telescoping" together of the functional differentiation might perhaps be adduced as a possible explanation, since the walking movements start relatively later than they do in *Ambystoma punctatum*, but in the case of the hind limbs in *Triturus* this is just the reverse: here the walking movements start in a certainly not later, but probably earlier stage of bodily development.

The primitive coordination of the limb movements in walking in *Triturus* and in the Axolotl is apparently of a nature different from that in *Ambystoma punctatum*, a statement which is supported by the demonstration of coordination mechanisms acting directly between the limb movements in larval locomotion (parallel and diagonal coordination).

A last interesting point is the type of the initial responses. In this respect also considerable differences have been recorded between the three species. In order to increase our insight here it would be necessary to repeat the observations in *Ambystoma punctatum*, paying special attention to elevation movements. As yet any kind of unitarian explanation seems difficult. We restrict ourselves to mentioning the fact that adduction movements do not play a role in the initial responses of the Axolotl, in contrast to the two other forms.

VIII. SOME OBSERVATIONS AND EXPERIMENTS ON ADULT LOCOMOTION IN TRITURUS TAENIATUS

Some current notions about the terrestrial locomotion of Reptiles and Urodeles need critical experimental testing. Such notions are for instance: 1. that the ventral side of the body and tail are continuously in touch with the ground, 2. that the greater portion of the propelling force is provided by the tail, and 3. that the limbs do not move independently, but that their movements are integrated with the "primitive" sinuous trunk movements.

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[1] It would be interesting to know whether it does occur as a postural response in this form. Its absence as a spontaneous phenomenon might be related with the early appearance of the walking movements.

The first two points can be checked and disproved easily by lifting the tip of the tail during locomotion, and by observing the animals during rapid locomotion, in which usually body and tail are entirely lifted up from the ground.

With the third point interesting problems regarding coordination of limb movements are connected, which partly bear a relation to the researches carried out by the school of GRAY on the coordination of locomotor movements in Amphibia, although these researches are concerned mainly with Anurans. For instance, observing the slow terrestrial locomotion of *Triturus*, one sees that just as in Anuran walking a hind limb is protracted shortly after protraction of the contralateral fore limb. However, as was already mentioned earlier by GRAY and LISSMANN (1940), as soon as locomotion becomes somewhat more rapid, the diagonal pairs of limbs move exactly in phase.

Walking under water in *Triturus* is distinctly different from terrestrial walking. In the first place the trunk may be kept entirely rigid while the limbs make ordinary walking movements (although usually weak sinuous movements of the trunk are still seen). Often the diagonal pairs of limbs move exactly in phase, even during slow locomotion. The posture of the limbs as well as their movements are characterized by less flexure: the limbs are more stretched away from the body in the horizontal plane. Moreover the general impression of the subaqueous pattern is one of greater flexibility (i.e. less strict coordination) than that of the terrestrial pattern. The latter is continuous and stereotyped, it makes an impression of automatism, as of a mechanism which is running continuously until it is stopped by some external factor. Under water, on the contrary, an alternation occurs between periods of mobility and periods of almost absolute immobility. Here the fore limbs often make independent orientation movements, which are not coordinated with trunk movements, although the hind limb movements are still rather strictly coordinated with each other and with trunk flexions. The hind limbs are mainly functional in simple propulsion, whereas the fore limbs seem to be subject more directly to the influence of higher nervous centres.

On transfer of an active animal from land into water the "automatism" of terrestrial locomotion appears to be blocked, and the animal often at first becomes motionless. Under water the animals show less spontaneous activity than on land. If we let an animal walk in a large dish and add water slowly, the locomotion pattern does not change as long as, in case of a normal attitude of the head, only the lower part of the head is under water. Changes appear only when the region of the eyes comes under water, even if the back is still for the greater part above the water level. First the phase differences between the movements of the diagonal limb pairs become less and less. The sinuous movements of the trunk do not show a distinct decrease before the entire animal is under water. These observations apply only to the behaviour in the reproductive season, because in other seasons the urge to escape the water obscures the pattern.

The coordination in terrestrial locomotion is not as strict as would appear from the above description of the pattern. If an animal is made to climb against a wet perpendicular glass wall, or if it tries to walk on a wet glass plate while being held by the tip of the tail, it frequently happens, probably as a result of the increased propulsion drive, that the coordination pattern undergoes a similar change as described previously after amputation of both fore limbs: during several successive diagonal cycles the hind limbs may be regularly protracted before the fore limbs. This occurs even during slow locomotion, when normally the phase differences between the diagonal limb pairs are most pronounced.

In order to avoid confusion it must be stated here that, contrary to previous researches carried out with spinal Amphibians, we have certainly to do here with highly voluntary patterns of movement. To make out which parts are played proportionally in the locomotion pattern by voluntary and involuntary mechanisms has not been the purpose of this paper, but this will certainly have to be investigated later (see also page 507).

The first aim of the experiments to be described has been to acquire a better understanding of the factors which determine the differences between the terrestrial and the subaqueous patterns of walking. Three of these factors have been tested tentatively. First of all the weight of the animals was altered by putting on little weights made out of lead plate, or by partly suspending the animals horizontally by means of string loops. In the second place the influence of the specific weight of the medium was tested by using either paraffin oil (sp. w. 0.87) or olive oil (sp. w. 0.92) instead of water as a medium. Finally the external resistance was altered in two ways, in terrestrial locomotion by using a mercury surface as an underground, and in subaqueous locomotion by adding about 50% of chick albumen to the water (by the results of the latter method also the possible "viscosity effect" of the oils used could be distinguished from their actual "specific weight effect").

Some results and preliminary conclusions will now be briefly represented. First of all there is the question which factors determine the stereotyped character and strict coordination of terrestrial locomotion. It might easily be thought that this is due simply to the contact with a solid underground, by which the different parts of the moving body are fixed in relation to each other. However, it appeared that the same characteristics of the pattern may also occur in animals suspended in oil without touching the bottom. At the same time oils eems to condition the same "automatism" of the pattern which is observed on land. Locomotion in oil tends to be continuous without breaks, and does not even stop before obstructions. The albumen solution of about equal viscosity does not produce such effects.

One might also think that the weight of the animal (either the absolute weight, on land, or the relative weight in a fluid medium) might influence the pattern, through perception either by tactile or by pressure sense organs of the ventral skin, or by the proprioceptors of the legs. This, in fact, is the first explanation one thinks of on observing the differences between the terrestrial and the subaqueous locomotion pattern. That it is probably not true is indicated by suspension experiments, in which the influence of the weight is eliminated, and even, under certain circumstances, the influence of tactile stimulation of the legs (suspension in oil) without resulting in an alteration of the terrestrial pattern. On the other hand it seems impossible to imitate the terrestrial pattern under water by increasing the weight.

From the above we must conclude that the specific weight of the medium, in other words the air pressure or hydrostatic pressure determined by it, must be perceived directly. Which sense organ or organs are involved in this kind of perception is still an open question. At any rate the animal is able to distinguish very clearly between a medium with a specific weight of 1.0 and one with a specific weight of round about 0.9. As mentioned above, a medium of the latter specific weight conditions a pattern which strikingly resembles the terrestrial pattern in several respects.

Turning our attention to a single separate feature of the locomotion pattern, the sinuous movements of the trunk, our results are the following. On lifting the walking animal from the ground or on transferring it from land into water, the sinuous movements become weaker. On the other hand, during locomotion both in albumen solution and on a mercury surface the sinuous movements usually are markedly stronger than they are in the same animal in water. It is suggested, therefore, that the sinuous movements become stronger under circumstances which make locomotion more difficult. Such a circumstance is for instance high friction with the underground or with a highly viscous medium, but also too low friction with the underground, as occurring in the case of the mercury surface. An interesting question would then be, in which way the animal would be able to determine the "degree of difficulty" conditioned by the medium.

The phase differences between the movements of diagonal pairs of limbs, regularly occurring during slow locomotion on land, may also occur, although more incidentally, in the other media investigated and on the mercury surface. The fact, however, that they are always less pronounced on the mercury surface than in the terrestrial locomotion pattern of the same animal, suggests that they may be accentuated by contact of the limbs with an underground which offers some resistance.

Finally it must be mentioned that "swimming" movements with actively adducted limbs have been observed to occur regularly during locomotion on a mercury surface and in animals suspended horizontally and free from the ground. Apparently these movements may occur wherever there is a lowered external resistance. They may therefore not be regarded as specifically aquatic, but must be seen as a general consequence of an urge for fast locomotion.

IX. SUMMARY

1. A descriptive study has been made of the responses and spontaneous movements of the developing limbs of larvae of *Triturus taeniatus* and *Ambystoma mexicanum*. The results are compared with the findings of Coghill (1929) in *Ambystoma punctatum*, and considerable differences are demonstrated. It has been found impossible to give an explanation comprising all these differences and at the same time not contradicting Coghill's views.

2. In both forms studied early limb movements of any type and of both fore and hind limbs may be, from their very first appearance onwards, altogether independent of any visible action of the trunk musculature. There is no evidence for the existence of a "total pattern" in these forms.

3. The spontaneous alternating locomotor movements of the larval limbs usually do not show integration with trunk movements, not even at their first origin. In the fore limbs, the appearance of these movements is preceded by a spontaneous, pre-ambulatory pattern of usually well integrated limb and head movements (see Fig. 1 C), a phase which in *Ambystoma punctatum* is apparently altogether missing. The pattern in question is essentially the same as that exhibited by the animal during turning around a vertical axis. The coordination between limb and head movements underlying this pattern is opposite to that operative in initial spontaneous locomotion in *Ambystoma punctatum*.

4. The coordination between fore and hind limb movements in both forms studied is also independent of trunk movements. It is apparently acting directly between the limbs, instead of taking the form of a "total pattern" in which the "swimming" movements of the trunk constitute the dominant factor (Coghill). Evidence is brought forward

for the existence, during the early development of coordination, of a "parallel" coordination mechanism acting between ipsilateral limbs, and preceding in origin the "diagonal" coordination mechanism known from adult locomotion (see Fig. 1 D).

5. Tentative experiments in adult locomotion of *Triturus* have led to the following conclusions:

a. The coordination pattern may be altered experimentally in several ways. Whether such alterations are of a mainly involuntary or of a more voluntary nature remains to be settled.

b. The differences between the terrestrial and the subaqueous locomotion pattern are apparently due to differences in specific weight of the medium, which differences must be perceived directly. It is not known which sense organ is functional in this perception.

c. Notably, the strict coordination of the movements in terrestrial locomotion is not due to the contact with a solid underground, as was thought previously.

d. The sinuous movements performed by the trunk during locomotion, in general become stronger when locomotion is more difficult. This may be caused by increase as well as by decrease of the external resistance.

e. "Swimming" movements of the trunk, accompanied by active adduction of the limbs, not only occur in fluid media, but wherever the external resistance is low.

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COMPTES RENDUS DE LA SOCIÉTÉ NÉERLANDAISE DE ZOOLOGIE

JANVIER 1953 – DÉCEMBRE 1954

Séance du 14 février 1953 à Amsterdam

L. DE RUITER (Groningue). The function and evolution of animal colour patterns.

The main function of animal colour patterns is to influence the behaviour of other animals. Those may be members of the same species as the adapted animal (its parents, young, sex partner, rival, etc.), or belong to another species (preys, predators, etc.). An extensive review of the importance of adaptive coloration in predator-prey relationships was given by COTT (1940). Taken as a whole, the evidence collected by this author leaves no doubt of the widespread occurrence and high protective value of such adaptations. This evidence, however, is for the major part indirect, being based on such arguments as divergence in the patterns of related species living in different environments, convergence in the appearances of non-related species living in the same habitat, and correlations between the occurrence, in different species, of certain patterns and the possession of special traits, such as inpalatability or a special type of behaviour. Direct, conclusive proof on the protection afforded by adaptive colour patterns can be derived only from observations of encounters between living animals in essentially natural surroundings. This is a laborious work, and such studies are still small in number. Yet several of the main points of the theory of adaptive coloration have been confirmed in this way. Direct evidence is now available, for instance, (1) for the protective value of colour resemblance in camouflage, (2) for that of mimicry of an inedible species by one that is palatable, and (3) for the relative inpalatability of conspicuous forms. In recent years progress in this field has continued. In an important series of experiments, POPHAM (1941–1947) has made a first step towards better quantitative investigation of the survival value of camouflage. Further, direct observation has on one more point (countershading) given some support to the conclusions based on circumstantial evidence (DE RUITER, 1952). Several important studies have also been made on the functional value of colour patterns in intraspecific relationships, e.g., that by TINBERGEN & PERDECK (1950) on the significance of the red patch on the adult Herring Gull's bill for the begging response of the chick.

On the whole, the conviction is steadily gaining ground that the survival value of colour patterns is often very high, far higher than had been assumed originally, and that this is sometimes true even of patterns which have been regarded for many years as entirely functionless, e.g., the banding of *Cepaea* (CAIN & SHEPPARD, 1950).

Another interesting point is that the evolution of colour patterns sometimes seems to proceed very rapidly, not only from the evolutionary but also from the human point of view (for examples of changes in coloration that took place in a century or less, see HUXLEY, 1948). This makes the evolution of colour patterns a promising subject for research. In all investigated instances of rapid evolution in animal colours, the evolving character was found to depend on a single gene.

For most of the present discussion we shall restrict ourselves to these genetically simple cases. A population in which such a character is evolving will contain two forms of the gene governing it, and the relative frequencies of the two alleles will change from generation to generation.

At first sight, four factors come to mind as possible causes of such a shift in gene frequencies, viz., migration, mutation, selection, and drift (chance fluctuation).

(1) Migration and the consequent import of genes from other populations, in most cases prove to be far less intensive than might at first be expected. As a rule, it soon becomes clear that this factor cannot be responsible for the observed change in gene frequencies.

(2) Mutations occur at such low frequencies that they cannot be responsible for these rapid changes either.

(3) Selection, therefore, is the only agent that can be the cause of the observed shift in gene frequencies, because

(4) Drift can hardly be effective unless the populations are quite small, and even more important, unless the two alleles do not markedly differ in survival value.

Whether or not natural selection could operate at an intensity high enough to cause the very rapid shifts in gene frequencies, has long been a subject of controversy. Recent work (e.g., SHEPPARD, 1951), however, suggests that this is well within the realm of possibilities.

So far we have discussed the transient polymorphism of evolving populations. Valuable results can also be obtained by a study of cases of stable polymorphism, in which the relative frequencies of the different types are constant. First of all, data on the intensity of selection can be derived from the study of the factors that maintain the polymorphism. Secondly, interesting facts have been found in many mimetic species (Ford, 1937). Here it often appears that the presence or absence of a complicated mimetic resemblance depends on a single gene. Further analysis shows that this must be due to the selection of a gene complex which modifies the phenotypic expression of the "main" gene in such a way that the main gene alone can "switch on" the whole complicated set of characters that constitute the resemblance.

The latter example already forms a transition to the cases where colour adaptations depend on the co-operation of many, more or less equivalent genes. Very little is known about either the genetics or the evolution of such adaptations. However, such data as the comparative anatomy and ontogeny of these patterns have provided, seem to be compatible with the hypothesis that here, too, natural selection has been the main agent in the evolution of the adaptations.

The following general picture seems to emerge from the available data. The origin of the manifold adaptations in the colour patterns of animals is due to natural selection of certain gene combinations from the material supplied by mutation. This selection appears to be a very powerful, fast working agent, enabling populations to adapt their colour patterns to changes in environment with relatively little time-lag.

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Séance du 10 avril 1953 à Utrecht

1. S. Dijkgraaf (Utrecht). Central integration of sensory stimuli.

Active movement of almost any animal will evoke stimulation of some of its sense organs (e.g., tactile endings, muscle spindles, labyrinthine sense organs, the eye, etc.). Recently several investigators independently put the question whether – and how – animals are able to discriminate between these self-generated and the normal, externally caused sensory stimuli (Buytendijk, Dijkgraaf, v. Holst & Mittelstaedt, Sperry).

The fact that animals are able to do so follows from the simple experience that they can use their sense organs not only when at rest, but equally well when they are in motion. A minnow, swimming restlessly up and down in its container, will react immediately to a slight artificial pressure change, although the animal had been constantly subjected to all kinds of self-generated pressure changes (DIJKGRAAF, 1941). From this fact and a great number of similar observations it must be concluded that animals rather generally "know" exactly the whole complex of sensory stimuli which is to be expected when moving actively. These stimuli are not used by the animal, but only centrally neutralized; they do not release any reactions under normal circumstances.

Only under artificial circumstances stimulation due to active movement may release reactions. This will occur in all cases in which the normal relation between active movement and the corresponding self-generated sensory stimulation is disrupted, either by alteration of normal movement or by alteration of normal sensory function. Examples of the first case are v. BUDDENBROCK's experiments and those of his collaborators, making him believe that insects and crabs may show optomotor reactions caused by self-generated retinal stimulation (see for details DIJKGRAAF, 1953). In reality the animals did not react to their self-generated stimulation but to the unexpected deviation from this stimulation caused by the passive movement inflicted upon the animal. Disturbing normal sensory stimulation by inversion of head or eyes releases strong optomotor reactions for the same reason (MITTELSTAEDT, SPERRY).

From the fact that animals must "know" exactly all self-generated stimuli in order to be able to use their sense organs for detections of externally caused stimuli it follows inevitably that SHERRINGTON's so-called "proprioceptors" cannot be of any use in giving the animal information about its own active movements. In fact, they are exteroceptors like the eye and ear! Derangement of posture or movement following deafferentation may be caused *a*, by elimination of the tonic influence originating in many sense organs (which is a thing quite different from their perceptive task) or *b*, by disruption of the normal relation between active movement and the corresponding self-generated sensory stimulation. The latter case is quite comparable to the abnormal behaviour of an animal with inverted head or eyes; yet nobody will conclude that the eyes act as proprioceptors in that case. So one should neither do here.

The second question as to how self-generated stimulation is distinguished from externally caused stimuli is still open. The "Reafferenzprinzip" (v. HOLST & MITTELSTAEDT) is hardly more than a statement of the facts mentioned in a clear diagrammatic form. Nevertheless this simple diagram has already shown its usefulness in clearing up several observations hardly understandable on terms of classical reflex physiology. A detailed account of the whole problem will be published in Experientia.

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2. G. P. Baerends (Groningue). The influence of central nervous mechanisms on the reaction to sensory stimuli.

There are two ways to study the capacities of the sensory organs: 1. leading off action potentials, 2. watching the reaction elicited.

The behaviour elements used as criteria in the second method are very often innate motor patterns ("Erbkoordinationen"; Lorenz, 1950), or behaviour elements of higher integration.

According to Lorenz the "Erbkoordination" is characterized by its constant and genetically fixed form and by the fact that it is released by the perception of a very definite stimulus situation. Moreover, however, the intensity of the movement is variable even under constant external conditions and the animal strives for finding the stimulus situation releasing the motor pattern. Both latter properties, according to Lorenz, indicate the presence of an internal stimulus production independent of the external releasing situation. Lorenz compares this phenomenon with the locomotory automatisms studied by von Holst (1937).

Different motor patterns are grouped together in a hierarchical system of instincts of different order (Tinbergen, 1951). Activation of such an instinct means that motor patterns belonging to it can now be released if the animal meets the appropriate situation. In general one may say that the instincts of different order are able to produce stimuli that act as afferent stimuli to a lower centre.

Therefore, at every level of the hierarchy we must reckon with 3 kinds of stimuli influencing the centre of the reaction: afferent external stimuli coming from the sense organs, afferent internal stimuli coming from a higher hierarchical level and efferent internal stimuli produced in the centre concerned.

We have seen that impulses are only transferred by this centre after the perception of a definite stimulus situation. This situation (especially when it is innately known) consists of only a few of the numerous characters of the adequate object perceptible for the sensory organs. The releasing value of the situation does not primarily depend on which of these key stimuli are present but of the total releasing value they are representing (law of heterogeneous summation). The various key stimuli co-operating in releasing a definite reaction differ in releasing value. One could say that each kind has a certain basic value around which variations are possible in accordance with the intensity in which the key stimulus is present. The sign stimuli have a configurational nature ("Gestalt"). Working up along these lines the different stimuli from the sense organs must be the task of a central nervous mechanism. We call this hypothetical mechanism the innate releasing mechanism (I.R.M.). This mechanism is one of the factors hindering the study of sensory capacities by means of behavioural reactions.

The internal stimuli mentioned above are a second factor interfering with such a study. These stimuli may work through or independent from the I.R.M., further analysis is needed to clear up this matter. At this moment there are arguments suggesting that both occur.

An attempt to obtain a quantitative picture of the collective action of external and internal stimuli on the performance of behaviour elements was made in collaboration with R. Brouwer and H. Tj. Waterbolk, using the fish *Lebistes reticulatis* during its courtship. When courting, this fish shows patterns of black markings that change according to the intensities of the different drives activated in the animal. One can use the marking pattern as an indicator for the strength of internal motivation. The external situation could easily be varied quantitatively by offering females of different size to the male, the bigger the female the stronger the stimulus. In the experiments a male was left together with a female until its markings had developed a definite phase. Then the female was suddenly exchanged for a female of known size presented under standard conditions in a glass tube and the reaction was studied. In this way curves could be drawn representing all points where a certain value of the internal stimulation together with a certain value of the external stimulation resulted in the same reaction. These curves roughly resembled a hyperbole (internal stimuli $\times$ external stimuli $= c^2$). The greater this combined stimulation the higher the intensity of the reaction. Higher stimulation also led to more advanced activities in the series of courting performances.

A second possibility to investigate the influence of internal stimuli on the reaction to an external situation, offered a study of the I.R.M. releasing the egg retrieving movement in the Herring Gull. These experiments were carried out in collaboration with G. J. Blokzijl, H. Groenewold, and J. P. Kruijt. We will restrict ourselves here to the experiments for testing the value of the feature "egg size". In each experiment 2 egg models of different size were offered simultaneously to the gull on the edge of its nest (the nest containing 1 egg model of normal size). A long series of experiments shows significantly a preference for the biggest egg even if this is of supranormal dimensions.

However, in many cases still the smaller of 2 eggs is chosen first. A closer analysis of these "wrong" choices proved to be very instructive in getting an insight in the internal factors influencing the reaction. Three different categories of these choices could be distinguished:

A. There are some individuals choosing consequently the smaller egg. In these gulls the fleeing drive appeared to be relatively strong in comparison with the brooding drive. (The eggs on the edge of the nest represent a situation fitting to I.R.M.'s of motor patterns of both motivations.)

B. All animals show at times a marked preference for either the right or the left egg or for the egg that is lying at a very special place. It is suggested that this might be a case of adaptation of the I.R.M., a phenomenon first discovered by PRECHTL when studying the gaping reaction of nestlings of song birds. The phenomenon appears mostly after many experiments with the same animal, it is quantitative in such a sense that a preference only for place can be broken and succeeded again by a preference for the bigger egg by increasing the size difference between the 2 models offered.

C. Sometimes the gull seems not to choose at all, it retrieves very quickly just at random. There is strong evidence that in such gulls the brooding motivation had reached a very high intensity. Under comparable conditions PRECHTL too found decrease of selectivity of the gaping reactions of song birds.

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3. L. DE RUITER (Groningue). The measurement of the "prey value" of preys.

The behaviour of animals is influenced by stimulation of their sense organs. The first step in the analysis of this phenomenon must be a careful quantitative description of the relation between the pattern of sensory stimulation and reaction. Some work in this field has been done by ethologists. The first, now widely known result was the discovery that the reaction of an animal to a given external stimulus depends on the internal state of the animal. This has led to the formulation of the concept of drive. On the other hand, at a given level of the drive for a certain activity, the frequency of that activity varies with the nature of external stimulation (N. Tinbergen, 1952).

We shall discuss here the value of the experimental data on the latter point for the explanation of the influence of sensory stimulation on behaviour, taking observations on feeding behaviour as an example. The reason for this choice is that more work has been done on feeding than on any other activity, as this aspect of behaviour interests not only ethologists but ecologists as well. Hence, the following remarks also have some bearing on ecological problems, into which, however, we cannot enter now.

Any object to which an animal may react with a feeding response will be called a prey. In an experiment equal numbers of two or more different types of prey are offered to a predator. The frequency of the feeding responses evoked by a certain type of prey under given circumstances will be called the prey value of this type under those circumstances for the predator used. We shall restrict ourselves to the visual perception of preys. Most animals will show feeding responses (or at least the first links of the reaction chain of which such responses consist, viz., hunting and catching) to a wide variety of objects, as long as their size and their type of movement remain within certain rather wide limits.

In the work published so far, prey values have not been given in absolute numbers, but as relative prey values (R.P.V.), the value for one of the types of prey used in the experiment being chosen as unit.

Three factors, apart from the intrinsic properties of the preys, were found to influence their R.P.V. Sometimes the R.P.V. did not vary with the degree of activation of the feeding drive, e.g., in the work of Popham (1941, 1943) with fish preying on water bugs. In other cases, however, such as in Drees' (1952) experiments with Salticid spiders as predators, hunger proved to have a definite influence on the R.P.V. This difference in results is probably due to the fact that different characters of the preys were investigated in the two cases. Drees studied the influence of size on prey value. Probably the largest preys offered by him released not only feeding but also flight in his spiders. Hence, the frequency of feeding responses in his experiments will have depended on the relative levels of excitation of feeding drive and escape drive. The higher the feeding drive, the longer it would be able to block escape, even in the face of strong releasing stimuli, and, therefore, the wider the range over which the prey value will increase with the size of the preys. In Popham's experiments, on the other hand, probably only the feeding response of the fish was affected by the difference among the various types of prey used (different degrees of tone contrast with their background).

A further important point that came to light in Popham's work is that the relative prey value depends on the prey density (i.e., the number of preys per unit volume), except at very low densities. At a certain, rather high density the relative prey value of the highest rated prey reaches a maximum. If the density is still further increased, the R.P.V. decreases again. We shall not discuss the latter phenomenon here. As regards the initial increase of the R.P.V., the following explanation seems plausible. A predator will not notice a prey if separated from it by a distance greater than the distance of perception (Laing). In other words, each prey is surrounded by a spherical danger zone with this distance as its radius. As the prey density increases, the danger zones will overlap more and more. That is to say, the predator will more and more frequently see two preys of different type simultaneously. In such cases it will, as a rule, pursue the highest-rated prey, thereby giving the other a chance to escape. Obviously, the influence of this factor on the R.P.V. is difficult to evaluate. It is essential, therefore, to make experiments at such low densities that no overlap of danger zones occurs.

Another factor that may materially alter the R.P.V. of a prey for a predator are the previous experiences of this individual predator (de Ruiter, 1952, 1953; L. Tinbergen, 1948).

It follows from the above that experimental data on prey values can only be useful for the quantitative explanation of the relation between sensory stimulation and reaction, if the following three conditions are fulfilled: (1) information must be given on the degree of hunger of the predator, by mentioning not only relative but also absolute response frequencies; (2) the prey density must have been sufficiently low to exclude overlap of danger zones; (3) the fullest possible account must be given of the previous experiences of the predator. None of the papers published so far contains information on all three of these points. In other words, the study of the problem has hardly advanced beyond the qualitative stage.

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Ruiter, L. de, 1953: Levende Nat., **56,** 41–48.
Tinbergen, L., 1948: Vakbl. Biol., **28,** 217–228.
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4. J. de Wilde (Wageningen). Mechanisms of communication in the honey-bee colony.

Contacts with congeners play an important role in the relations between animals. This is especially true for communities in which division of labour occurs. The bee colony forms an impressive example in this category. A bee colony may be considered as an organism of a higher order, several physiological functions of bees having an individual and a social aspect.

Between the members of the bee colony, as between the cells of organisms, co-ordinating and regulating mechanisms are present. These mechanisms may have an animal or a vegetative character. The first-mentioned are based upon sensory communication, the latter, maintaining conditions for a longer time, probably have a material (hormonal) base.

In the following, the "dances" of field bees, related with colony nutrition, wil not be treated in extenso, as they have been reviewed recently on several occasions. With many other social functions (cleaning, care of larvae, respiration, temperature-regulation, defense, swarming) co-ordination is of no less importance. In what follows the stress will be laid upon what is known of these types of communication.

A. Communication between worker bees.

a. In feeding experiments with a sugar solution, to which traces of P^{32} were added, RIBBANDS found that an extensive communication is obtained by food distribution within the colony. Already after two hours, half of the field bees had become radioactive, and after 48 hours nearly all the bees and larvae had become so.

The supposition of RIBBANDS that food distribution plays an important role in the division of labour, could not be confirmed by the observations of LINDAUER. The latter studied the activities of individual worker bees throughout their life. In contradiction to the findings of RÖSCH, LINDAUER found that a worker bee may carry out two or more types of activity at any given age, e.g., cleaning the cells and feeding the larvae. Continuous observations of individual bees showed that between periods of activity, periods of rest on the combs may occur, alternating with lengthy "patrol" periods during which the bees probably find out for themselves what tasks require their attention.

Food distribution may be of great importance for the regulation of female dimorphism (see B). Field bees that "drift" to other colonies may offer food to the defenders of these, as a part of "submissive" behaviour" (BUTLER).

b. The "dances" of field bees will not be treated in extenso. The tactile and olfactory senses (antennae) play the main role in this type of communication; location and smell of the food-source are indicated by means of this "language".

c. During "scent-fanning" bees emit a specific odour, which is produced by the gland of Nasanoff, on the abdomen. This behaviour occurs in situations in which bees are disorientated, e.g., during swarming or after displacement over a considerable distance. At the hive-entrance the fellow-workers are recognised by their odour. An odourless food-source will be provided with a "scent-marking" which works quite efficiently. The specific odour depends upon the composition of the food, and may change within a few days (splitting of a colony; RIBBANDS, KALTOFEN).

B. Communication between workers and queen.

The "royal train" suggests intensive communication between workers and queen. This continuously changing group of workers feeds the queen and leads her during oviposition. Under these and other circumstances it appears that the queen emits an attractive scent. The presence of a queen inhibits ovarium growth in worker bees. This effect can only be brought about by direct contact between the mouth part of workers (experiment with seperation by one and two layers of wire gauze respectively; HESS). If a specific inhibitory substance would be at work, one could speak of a "sociohormone".

C. Communications between queens.

The piping sounds of queens form an entirely different type of communication, the function of which is apparently to prevent fights between queens. Both piping within and outside the comb is emitted in "strophes" of 2–4 sec., each of 5–10 short blasts.

The frequency of these sounds is 300–350 and 400–500 Hz respectively. They probably have the same origin, the first-mentioned being "damped" and deformed within the comb. The origin of the sound is very probably not in the wings (ARMBRUSTER) or the basal wingplate (SNODGRASS) but in the stigmata which together with the abdominal air-sacs function as a flute (WOODS). The mechanism of sound-perception is not exactly known. Specific organs of hearing are missing. Frequency discrimination is poor (HANSSON), queens answering to tunes of various frequencies (160–1300 Hz). A condition for sound-perception is contact with a solid substrate; the sounds are perceived through the vibratory sense.

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KALMUS, H. & C. R. RIBBANDS, 1952: Proc. roy. Soc., B **140,** 50.
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Séance du 16 mai 1953 à Leyde

1. E. J. Slijper (Amsterdam). On sounds emitted by Dolphins. Short lecture on what is known in literature about sounds emitted under water by whales and dolphins. Demonstration of a grammophone record of sounds of dolphins made by the staff of the Marineland Research Laboratory, Florida, U.S.A., by using a hydrophone.

Reference: Slijper, E. J., 1955: Vakbl. Biol., **35,** 193–200.

2. J. J. Laarman (Leyde). The host-seeking behaviour of the malaria mosquito *Anopheles maculipennis atroparvus.*

Voir: J. J. Laarman, thèse, Leyde, 1955.

3. L. W. D. Caudri (Paris). Exposé des travaux biologiques en Syrie.

Après une introduction traitant des difficultés générales que rencontre l'Assistance technique des Institutions spécialisées des Nations Unies dans les pays dits sousdéveloppés, des précisions furent données sur deux points différents:

A. Législation phytosanitaire. La coopération internationale s'efforce d'obtenir que les exigences phytosanitaires que posent les pays vis-à-vis des importations et exportations de végétaux et de produits végétaux soient justifiées du point de vue biologique. En Syrie une nouvelle loi a été adoptée qui se base sur la Convention internationale pour la protection des végétaux de la F.A.O. (Rome, 1929).

B. Insectes nuisibles au coton. Le ravageur le plus important des cultures de coton, assez récentes en Syrie, est *Earias insulata* Boisd. (spiny bollworm), dont malheureusement l'hibernation reste insuffisamment connue. Il est probable que vers l'automne les larves entrent en compétition directe avec celles de *Pectinophora gossypiella* Saund. (pink bollworm), ce qui expliquerait que cette dernière espèce soit assez rare dans les régions où sévit *Earias.*

Des essais de lutte chimique ont démontré que les poudrages, même s'ils sont préférés par les cultivateurs en raison de la pénurie d'eau, ne donnent que des résultats médiocres. Par contre, des résultats prometteurs ont été obtenus à l'aide de pulvérisations à haute concentration à base de toxaphène et de dieldrin et surtout d'endrin (produit 269) qui a permis de protéger les cultures pendant 10 à 20 jours.

Litérature: Programme élargi d'assistance technique, FAO Rapport, **110,** 1953, Rome.

Séance du 5 septembre 1953 à Oostvoorne

1. D. J. Kuenen (Leyde). La station biologique "Weeversduin" à Oostvoorne.

2. B. M. Lensink (Oostvoorne). Ecologie de la distribution des sauterelles.

Les résumés de ces conférences n'ont pas été remis au secrétaire.

Séance du 7 novembre 1953 à Utrecht

Conférence sur la connaissance et l'acquisition des faits dans l'instruction biologique des écoles secondaires de la Hollande.

Voir: Vakbl. Biol., **34,** 129–139, 145–154.

Séance du 12 décembre 1953 à Amsterdam

1. N. Postma (Utrecht). General bases of structural properties and mechanical functions of muscles.

Simultaneous with the continuation of research on the mechanical properties of muscle, important investigations on the chemical processes in muscles took place during the period between the two world wars (Meyerhof, Embden, Parnas). While this work was at its summit, the interest of biochemists (von Muralt, Weber, Szent Györgyi, Astbury, Dubuisson) became focused on the properties of muscle proteins and on the influence of ATP on these properties (Engelhardt, Needham, Szent Györgyi, Weber).

Weber, reviewing the results obtained in this field, made use of the published data on physical and chemical properties of a dozen isolated fibrillar muscle proteins and of six combinations of two of these; he succeeded in clarifying the confused terminology, thereby elucidating the whole problem. He was also able to eliminate the factors causing excitability of the muscle from the contractile system. Moreover, he could establish the conditions which need to be satisfied to allow the results of experiments on models to be related to the functioning of the muscle elements. Finally he has found that ATP not only furnishes the energy for the contraction and for tetanus (during which ATP is split by the muscle), but is also active in unchanged form, by governing the grade of structure of the muscule: lack of ATP causes extreme rigor (fixity), making relaxation impossible, and reversely excess of ATP causes extreme flaccidness, rendering the system powerless. It is now certain that in muscle, next to the "phasic" active principle a structural function is inherent, which must be identical with the so-called viscosoid tonus, studied by Jordan. Both functions are based on an interaction between ATP and actomyosin (= the combination of actin and myosin, two of the isolated muscle proteins). The latter substance is present in all muscles, if not in all organs and organellae (Hoffmann-Berling), e.g., the protoplasma of *Amoeba* (Ranzi), functioning in movement and posture. Actomyosin, together with ATP and magnesium, governs the structural properties and the mechanical behaviour of muscles and organs.

Not only actomyosin-sol and -gel respectively, or threads drawn from the latter, can be used for experiments on models, but such experiments can also be made on simplified muscle fibres, provided that the substances added to the experimental milieu can reach the axis of the object unchanged within a reasonable time. Moreover, the object should be firm, but not too rigid, and by making the muscle fibre free of potassium, the contraction-cycle must be separated from the stimulation-mechanism. The protein content of the thread of actomyosin should be low. In both preparations a certain thickness should not be exceeded. Moreover, ion-concentration, temperature and the diameter of the particles (lower than the maximum allowed) should be identical, to ensure comparable results.

From experiments on such models and on fibres of smooth and striated muscle it is evident that the muscle contraction initially goes slowly (and also the development of tension), and that a considerable shortening (80 %) can be reached. Because of its more differentiated structure, the skeletal muscle is quicker (15 ×) and stronger at the expense of the attainable shortening (30 %). WEBER is of the opinion that the smooth muscle contracts better than the skeletal muscle. However, if we apply the data obtained by BUCHTHAL to the results of WEBER's calculations, we obtain the following:

The specialisation of the skeletal muscle is expressed in the distinction between anisotrope discs (A), alternating with isotrope discs (I); in the middle of the latter lies the Z-membrane (one compartment between two Z-membranes corresponds to one BOWMAN's disc). The A-disc forms 65 % of the volume of the fibrillae and since these in their turn form 60–80 % of the muscle fibres, the A-disc forms 40–55 % of the latter. The actomyosin content is 70–75 % of the volume of the fibres. WEBER concludes therefore that the actomyosin is not all contained in the A-discs. Differences in double refraction and in electron-transradiation of A- and I-discs indicate the presence of a continuous cover of the actin-filaments, which are, exclusively in the A-discs, filled up with myosin. BUCHTHAL found that the I-disc can be lengthened for 43 % by contraction of the neighbouring A-discs. WEBER found a primary shortening of actomyosin at 80 %. An A-disc of 12,500 Å will thus contract to 2,500 Å; simultaneously the I-disc will be stretched from 7,500 Å to 10,000 Å. The length of one BOWMAN's disc will therefore recede from 20,000 Å to 13,000 Å, which represents a shortening of 30 %; this value was actually found by WEBER for the whole muscle fibre. The A-discs therefore can be just as contractile as the primitive smooth muscle fibres, but the effect is lessened by the extensibility of the non-contractile I-discs. The elasticity of the latter causes intrafibrillary tensions that may contribute to the fast relaxation of skeletal muscle (together with the fixed antagonism). For the smooth muscle fibres this force must be looked for only outside the fibre; elasticity of compressed elements and the pull which is exerted on the muscle from outside.

There are therefore two components in the function of movement and posture of the muscle: the phasic component is more important for the first, the structural for the second. In the smooth muscles it is the structural component which predominates most often (JORDAN); in the striated muscles it is the phasic one which comes to the fore. Till now this last one has been considered in England and America to be the only one, cf. lately LOWY. However, the part played by each varies considerably according to the function of the muscle being more for movement or for posture, whereas also the season, the prae- and postnatal life and the ionic composition of the (external) medium have big influence (WACHHOLDER). It would take too long to illustrate this point with examples.

It is now possible to give a general basis for the physiology of muscles, and to regard deviations therefrom as functional specialisation.

Reference: WEBER, H. H., 1952: Ergebn. Physiol., **47,** 369–468.

2. D. J. KUENEN (Leyde). Sur la gestion de l'eau des Isopodes terrestres.

Cette conférence sera publiée bientôt dans le périodique Archives néerlandaises de Zoologie.

Séance du 6 février 1954 à Amsterdam

N. H. SWELLENGREBEL (Amsterdam). Wild, domestic and interhuman parasitism.

Voir: Docum. Med. Geogr. Trop., **7,** 182–191, 1955.

Séance du 15 mai 1954 à Leyde

1. A. C. PERDECK (Leyde). Quelques expérimentations sur l'orientation des oiseaux.

Voir: Jversl. Vogeltrekst. Texel, 1948–1953.

2. J. W. SLUITER (Utrecht). Sur le mécanisme de la mastication des Chiroptères. Conférence illustrée avec un film démonstratif.

Voir: Ned. Tijdschr. Geneesk., **98,** 2866–2867.

Séance du 24 et du 25 septembre à Groningue

1. G. P. BAERENDS (Groningue). Le laboratoire zoologique de l'université de Groningue.
2. L. DE RUITER (Groningue). Le centre respiratoire des poissons.
3. Mlle B. BAGGERMAN (Groningue). Sur l'influence de la durée des

journées et de la température sur le cycle reproductif de *Gasterosteus aculeatus*.

4. J. METUZALS (Groningue). Les aspects neurohistologiques de l'innervation de l'adenohypophyse.

5. L. TINBERGEN (Groningue). Conférence sur les aspects futurs de l'écologie.

6. A. E. VAN GIFFEN (Groningue). Le chien, l'animal domestique européen le plus ancien.

7. L. F. KAMPS (Baflo). Sur les recherches biologiques associées aux atterrissements.

Les résumés de ces conférences n'ont pas été remis au secrétaire.

Séance du 2 novembre à Delft

1. C. ROMIJN (Utrecht). Development of temperature regulation in the Chick.

Voir: Section papers of the tenth world's poultry congress, Edinburgh, 1954. Tijdschr. Diergeneesk., **75,** 719–746, 1950.

2. J. ISINGS (Delft). Les aspects histochimiques de la crue des cheveux.

Un résumé de cette conférence n'a pas été remis au secrétaire.

3. Madame E. H. HUECK-VAN DER PLAS (Delfgauw). Le virus polyédrique.

Un résumé de cette conférence n'a pas été remis au secrétaire.

4. Madame M. P. M. HERRMANN-ERLEE (La Haye). Sur des épreuves d'infection faites au moyen du virus polyédrique des teignes.

Un résumé de cette conférence n'a pas été remis au secrétaire.

5. H. J. HUECK (Delfgauw). Localisation et caractéristique physicochimique du virus polyédrique des teignes.

Un résumé de cette conférence n'a pas été remis au secrétaire.

ERRATA

In my recent paper "Aspects and Prospects of the Concept of Instinct (Vicissitudes of the Hierarchy Theory)" the following corrections should be made:

At p. 156, 6th and 7th line:
  Omit "Hinde (1953, 1954)".
At p. 178, 6th line:
  For "lowered" read "heightened".
At p. 247, 4th line from below:
  Omit conclusion (2).

A. Kortlandt